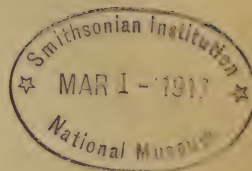


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XXVIII.—*On the Coloration of the Mouths and Eggs of Birds**.—II. *On the Coloration of Eggs.* By C. F. M. SWYNNERTON, F.L.S., F.E.S., C.M.B.O.U.

(Plate XIX. †)

PREVIOUS THEORIES.

HEWITSON wrote on the coloration of eggs in 1838, and remarked the common occurrence of uniform white in the eggs of species that lay in holes. I am unfortunately unable to state his further views here, or Seebohm's, as, through pressure of much work at the last, I left England without having looked them up. Prof. Newton ('Dictionary of Birds,' p. 188) says of Hewitson that "his remarks on the coloration of eggs have been frequently repeated, of course with more or less modification and verbose addition, by various plagiarists who have sometimes forgotten to mention the source of their information."

The only other theorist mentioned by Prof. Newton in this connection is Dr. McAldowie ("Remarks on the Development and Decay of the Pigment Layer in Birds"

* For Part I. see pp. 264-294.

† For explanation of plate, see p. 606.

Eggs," Journ. Anat. & Physiol. xx. 1886, pp. 225-227). Dr. McAldowie, starting on the assumption "that the pigmentary coat on birds' eggs came into existence at a very early period . . . and existed in the eggs of the progenitors of all the extant species," suggests "that its primary use is for protection from the solar rays, but that," the pigment being "unstable and variable" and change therefore easy, "it afterwards became modified for concealment." Finally, "eggs acquire a highly developed pigmentary layer, or lose their pigment entirely, according to whether they are exposed to the full glare of the sun or laid in situations inaccessible to its rays, and . . . the intermediate degrees of coloration are in direct ratio to the amount of light to which the eggs are exposed."

The theory might be regarded as receiving support from the fact that a considerable number of white eggs are laid in holes, and from such instances of apparent paling as those of the Jackdaw and Puffin. But it is interesting to note that there is no such additional pigmentation of tropical eggs as there is, apparently, of the skins of tropical mammals. Amongst tropical eggs it is interesting to contrast the deeply pigmented Nightingale-like eggs of *Cossypha natalensis*, laid in tree-hollows in the dark places of dense forests, with the cream or white eggs of *Chalcopelia afra* and *Colinus striatus* that are laid not only in an open nest in isolated, often semi-leafless, small trees or shrubs in grass-country at the hottest time of the year, but are quite commonly exposed to the direct sunlight. Prof. Newton gives a number of similar instances (*ibid.* p. 189), and many will at once occur to everyone.

Wallace's view ('Darwinism,' 1889, pp. 122-126) amounted to this:—All eggs were originally white. Those species that have continued to protect their eggs from direct observation—whether by laying in holes and domed nests, by covering the eggs when they leave, or (themselves possessing concealing coloration) by sitting close, or that, being powerful or fighters, keep good guard over them—have

naturally continued to lay uniform white or uniform pale eggs. In those species that have not thus concealed or defended their eggs, the latter have had to supply the deficiency by themselves (through Natural Selection) becoming concealingly coloured. A Song-Thrush's egg and a Plover's egg are both thus coloured, each in assimilation to a different environment; and small birds' eggs generally are regarded as concealingly coloured in relation to an all-concealing environment of complex lights and shadows. Doves' eggs are protected through the fact that "it is a difficult matter to discern, from beneath, whether there are eggs in the nest or not, while they are well hidden by the thick foliage above."

In brief, eggs with powerful parents and eggs concealed by extraneous obstacles to vision are white (or uniform pale), having been thus enabled to remain so; the others have developed concealing coloration.

The principle (of compensatory alternatives) that underlies Wallace's explanation is, I am convinced, the correct one. A species that lacks, for example, fighting-weight, must owe the survival of its eggs to their concealment in one way or another or to some other adequate defence or mixture of defences. Beyond this his explanation seems unsatisfactory. It is based on a sweeping generalization which is hardly, I think, supported by the facts. As Newton truly remarks and shows, by instances which might be greatly multiplied, no general rule can be laid down to the effect that eggs laid in holes and covered nests are of a uniform white. Numerous coloured eggs are found in such situations, and coloured eggs belong abundantly to powerful parents, while some coloured eggs are artificially covered in the parents' absence and others are closely covered by protectively coloured parents—for instance, the heavily and beautifully pigmented eggs of *Phyllastrephus flavistriatus*; this bird is the closest sitter I know. Conversely, there are white eggs that neither are shielded from the vision of their natural enemies, whether by close-sitting parents or other appreciable objects, nor possess

fighting parents—or any other special protection that we can see, unless it should be contained within themselves—*Colius striatus*, to take one example out of several. How account for the survival of these and the pigmentation of the others? It would seem that the first must possess some defence—some counteragent to conspicuousness—that we have overlooked, while the other class of case suggests that concealment may not be the only function of coloration in birds' eggs, though the pigmentation might in some cases be explained away as having unnecessarily outlived a period in which concealment by colour, and not its present defence, was the species' special protection.

Other points are overlooked in Wallace's explanation. It is the nest or nesting-hole, not the egg, of nearly all arboreal species that the enemy will specially look for and usually first detect. Having found it, he will not rest contented with trying "to discover from beneath whether there are eggs in the nest or not." If he is a natural enemy he will look in. And the nests of quite a number of species, as also many nesting-holes, tend to be, to a greater or lesser extent, conspicuous (especially in relation to the close search of an enemy), even when neither inaccessible nor the property of formidable owners. In any case, having regard to the habits of enemies, the line is drawn in the wrong place as between white eggs and all the rest. For numerous coloured eggs are also, as I wrote four years ago, "in brilliant contrast to the nests they lie in."

Finally, the argument that the eggs of most small birds lie in surroundings (of complex lights and shadows) that are capable of concealing objects of *any* colour might, indeed, account for the survival of coloured eggs, and even for the fact of their pigmentation, but it will not account for their specific coloration—for its diversity and for that quality of striking, even brilliant, distinctiveness which is so marked a characteristic of the eggs of birds.

To sum up, not only a number of difficult cases are left unexplained, but also the very thing which most requires an explanation.

PRESENT EXPERIMENTS.

In Prof. Newton's words, the subject was "worthy of much more attention than it has received." In July of 1911, while thinking out the general bearing of my results from insectivorous birds, I saw that they suggested the explanation for distinctiveness and diversity—in, at any rate, insects—that I have described in the first part of this paper: briefly, that most species are in varying degrees indigestible and liable to be refused when the enemy's gastric activity is insufficient to deal with them—that, therefore, there are relatively few species that do not require to be distinguishable at times from species that the enemy is at the moment hungry enough to digest.

Would the explanation also apply to the eggs of birds? occurred to me at first as an objection.

That it might be found applicable to the coloration of adult birds was rendered likely enough by the results of Marshall's experiments already referred to. There was no such evidence for eggs. Yet, working for some years with insects, I was already able to perceive that there is a close similarity between the phenomena of the coloration of birds' eggs and those of the coloration of butterflies, in spite of the fact that we have in the one case a generalized pattern and in the other a definite one, and to feel that whatever interpretation completely explained the one set would quite likely be found to fit the other. I had also met with eggs broken in the nest, not by the parents, yet uneaten. And the difference in flavour and consistency between, for example, Fowls', Ducks', and Plovers' eggs, even when cooked, suggested that at any rate a basis for possible preference on the part of enemies might be present. These and other considerations convinced me that the idea was at least worth testing.

I tested it in January and February 1913 on a lemur (*Galago crassicaudatus* Geoffr.) and a black rat. Attempts to secure other egg-eating animals were unsuccessful. The experiments carried out were sufficiently numerous and very

careful, and were based on the experience afforded by nearly seventeen hundred such experiments that I had already carried out in other directions. Both animals showed unmistakable preferences as between the eggs of different species. The lemur, it is true, showed them (like some few insectivorous birds) only when nearing repletion-point—an inadequate support for the hypothesis I was testing. The rat commenced to refuse certain eggs even when fairly hungry. And their preferences coincided.

Nothing could have been more marked than some of the contrasts between obvious repugnance and eager acceptance that occurred throughout the experiments on the rat. I wished, nevertheless, to suspend judgment until I should have tested the point on some other animal. A Butcher-bird (*Lanius collaris humeralis*) was secured later in the year, but it would eat no eggs at all except under pressure of great hunger. I had all along been particularly anxious to obtain some bird of the Crow family for these tests, an adult bird with wild experience, but I failed, both in Africa and, later, in England. They have been scarce latterly at Chirinda. A young Jay, which Mr. Seth-Smith was so good as to let me have from the Zoological Gardens (with the kind permission of Mr. Meade-Waldo, the original donor), gave me some very interesting preferences as between different species of earth-worms and of snails; but, to judge from its early mistakes even here (and from my experience of hand-reared nestlings generally), its education in egg-tasting would have entailed a wholesale robbery of nests that I should have been sorry to undertake. With a carnivorous mammal the experimenter is not confronted with this difficulty. Its choice (by smell and taste) is at all times so wonderfully unhesitating and accurate, that, to all appearances, it is partly instinctive. So, failing in an attempt to get a weasel, I used an Indian mongoose.

Genuineness of the Preferences.—The mongoose eagerly smelt or tasted every kind of egg offered it; but, from the outset, it resembled the rat in showing the strongest preferences—though probably none of the eggs tested were

disliked by it so greatly as was a Burnet moth. As in the case of the rat and the lemur, I carried out, not one, but several experiments to make quite sure that I was not suffering from self-deception, or the mougoose from some sort of misapprehension; and, as before, I sometimes used every sort of endeavour to *coax* the animal to eat the eggs it refused. It was my genuine endeavour (as it is always) not to prove my theory, but, if possible, to disprove it. In this I failed, and friends staying with us were equally struck with the strength of the preferences shown. One of these friends was Mr. Guy A. K. Marshall, my original guide and mentor, and the only person to whom (pending my own final satisfaction) I had yet mentioned the idea—in a letter written from Africa two and a half years before. In view of this fact—in view, too, of his personal experience in this kind of experimentation and of his acute faculty for criticism (well known to entomologists)—I was particularly interested and pleased to obtain from him an expression of his complete satisfaction as to the actuality of the preferences witnessed.

Indeed, the method employed admitted of no doubt. It was not a mere putting down of two or more eggs and seeing which was taken first, the animal being all the time prepared to eat the others too. Certain eggs left under the animal's nose were seen to be persistently ignored after tasting or smelling, while eggs of another species placed amongst them were each time at once picked out and eaten, the mougoose even, in the case of certain species, returning to the empty shell again and again, and licking it out afresh, or, in his eagerness, crunching it up, while still emphatically and obstinately refusing the rejected eggs, though these looked most tempting with their glistening contents brimming over the hole which I always made to avoid complications through varying strength of shell.

I wanted yet more evidence, however, and it was not till eight or nine months later that I finally decided to communicate my experimental results, and (with due reserve) the view they suggested to a meeting of the British Ornitho-

logists' Club*. Publication and discussion seemed, after all, at this stage, the best way to elicit any evidence there might be for or against. Several criticisms were made.

CRITICISMS.

I would like to make it clear that, if I discuss these criticisms somewhat fully here, it is done in no controversial spirit. I do so, partly because the fact that some of the criticisms were made at all shows that I was insufficiently explicit at the meeting, and I wish to be allowed to rectify my omission; secondly, because, even if we do not yet possess field-evidence in favour of preference in eggs, I can show that such evidence as exists is, at any rate, by no means incompatible with its existence, and I wish to make out a case for its fair and impartial consideration.

The two most important criticisms were:—

(1) The *unreliability of results obtained from captive animals*, and (2) The *lack of corroboration from field-observation*. It is a curious fact that it is just these two objections that critics have mainly used against the selectionist explanations of coloration in insects, that I had already been testing their validity in the latter connection for some years before I undertook my egg-experiments, and that I was to read a paper in which they were very fully discussed on the very next day. For a fuller statement than I can make here I would like to refer my readers to my paper read at a meeting of the Linnean Society on April 15, 1915.

(1) My experience in connection with the first objection has been that it is perfectly true that some animals in captivity mope, have capricious appetites, and are generally useless for food-experimentation. I have found, however, that these animals are easily recognised and eliminated, and that most animals give very consistent and reliable results—always provided that they are well cared for and tolerably happy, friendly with the experimenter, and provided with a rational diet. This should include enough of the class of

* Bull. B. O. C. xxxv. 1915, pp. 108–112.

prey that is being particularly experimented with to avoid an undue craving for it. Naturally the experimenter must also know the principles on which an animal feeds: my own early experiments, before I gradually learned these and discovered the various complicating factors that must be eliminated or watched for, were worth very little. He must realize that a hungry animal will eat almost anything that comes within the category of its natural prey, and not jump to the conclusion, when it does so, that it is necessarily indiscriminating at all times. He must know something of the animal's state of hunger at the outset and recognize the symptoms of growing repletion, must be able to follow the twists and turns of an appetite increased a little through ten minutes' fasting, decreased through a further morsel of food, or, it may be, stimulated suddenly by a specially savoury offering or depressed by an unsavoury one. And so on. It is insufficiency of knowledge on such points that has vitiated some food-experiments in the past and caused the results obtained sometimes to seem contradictory and unreliable. That the method may, carefully used, yield perfectly reliable results is indicated, I think, by the fact that in my own experiments wild insectivorous birds corroborated in the most ample manner the results I had obtained from captive birds, while totally unrelated carnivorous mammals (one of them unconfined) confirmed generally each other's verdicts on bird and mammal prey. That my egg-experiments only (and these the last to be carried out, with the precautions suggested by their predecessors) should, for some reason, be unreliable, is, indeed, perfectly possible, but not very likely, though they certainly require to be corroborated, as my insect-experiments were, in the field.

(2) "Non-corroboration from field-observation." In insects this objection has been brought against two views: (a) that birds eat butterflies; (b) that insectivorous birds have preferences. In each case the abundant results of specially-undertaken observation at once showed that the reason for the paucity of evidence had been a previous *lack* of special observation. Yet entomologists had had their

attention drawn for years to the scantiness of the evidence. How much more intelligible is it that we should have accumulated little evidence on a possibility to which our attention has never till now been drawn?

(3) *Acceptances were regarded as showing Indiscriminate-ness.*—As Mr. Jourdain very truly said, the Carrion-Crow devours all kinds of eggs. It would be surprising if it did not, for a hungry animal will eat almost anything that comes within the category of its natural prey. But this does not necessarily imply indiscriminate-ness. The wild bird on which I experimented most largely was an individual of *Dryoscopus guttatus*. When hungry enough, as it frequently was, it would readily accept the most nauseous insects I could offer it, and its acceptances of such extremely low-grade butterflies as the *Danainæ* and *Acreinæ*, witnessed by myself, perhaps nearly equal all other records put together—the very records on which critics have relied to demolish the theory of mimicry. Yet this self-same Shrike was a most discriminating bird! It only took two or three acceptances when it was at its hungriest to carry it beyond the *Acræa*-accepting stage, and, as it gradually filled up, it discarded species after species until, nearing repletion-point, there were only a few species left that it would accept at all. The same may be quite true of the Carrion-Crow.

Or, of course, it may not. Numerous insectivorous birds are as discriminating as the *Dryoscopus*. A few, however, fill up very considerably before they commence to discriminate—at any rate, in relation to certain large classes of prey. Some, again, are specialized to feed nearly to repletion on what are, to other birds, the most nauseous of insects. The case of the lemur suggests a likelihood of similar variation in digestive capacity amongst egg-eaters.

Mr. Stuart Baker mentioned that he had not experimented, but he had kept egg-eating birds and mammals and noticed no discrimination. My own non-experimental experience (though in another connection) was entirely the same as his, and I will use it to illustrate the difference between casual offerings and carefully-conducted experiment. Long ago I

had a Roller in my aviary. I frequently went in and fed it by hand. On a few of these occasions I offered that large, gaudy, evil-smelling locust, *Phymateus*. It was each time readily eaten. I also found it in the stomachs of one or two wild Rollers. I concluded, very naturally (and I believe I was rash enough to publish the conclusion) that Rollers are probably highly indiscriminating. A few years later I began definitely to *experiment* on Rollers. Then I found that, while they readily ate *Phymateus* up to a certain point in the satisfaction of their hunger, that point was by no means a very advanced one, and that from that point up to repletion-point they refused it with symptoms of dislike. Again, my mongoose sometimes left the eggs that formed part of his ordinary diet uneaten for quite a time. Had this occurred in the days of my first Roller I would have perceived no significance in the fact. The other fact, that they were always sooner or later devoured, would have satisfied me that they were all much liked, and the delay, if I thought of it, would have been put down to repletion. Had I experimented, I would sometimes have found (as I sometimes did find) that the mongoose was far from repletion and eager for food—but not as yet for that particular egg.

When told of acceptances, we should ask: how hungry was the animal? What went just before—was there, perhaps, special stimulation? Could there have been a special craving through the insufficient presence of that class of food in the everyday diet? Were not the eggs, perhaps, in any case all of a high-grade nature? Unless the first three questions can be satisfactorily answered, the acceptances, whether by wild animals or tame, are completely valueless as evidence of indiscriminateness. No number of unchecked records of eggs eaten can ever show that those eggs are not sometimes, perhaps often, refused.

Similarly, acceptances that are not seen to be accompanied by neglect or rejection of other species—or their relative immunity in the same locality—are quite useless as evidence of preference, and this is why such evidence must always be hard to procure in the field. It can only be obtained in

quantity by continuous watching and special experimentation.

4. *The Use of unsuitable Animals.*—This criticism was made of the offering of terrestrial eggs to a lemur and arboreal eggs to a rat. I had probably not been sufficiently explicit. I offered to each animal eggs of *both* categories, and each showed preferences in his own department, as well as confirming the other's preferences in his. The former fact is all that need really matter, and the additional confirmation was, at any rate, useful and suggestive.

The critic's point was that refusals of unaccustomed objects might be merely due to their non-recognition as possible food. Had a totally new *kind* of food been offered the criticism was perfectly sound, as I could quote numerous instances to show: horses transferred for the first time from an arid pasture to lucerne (Burt-Davy), nestlings reared on a very limited diet and dogs put on to a quite new food (my own observations), camels and natives of Jerusalem (Cyril Crossland)! But within the classes of food that they are accustomed to prey upon, wild animals are great experimenters, and, as anyone who has experimented much on them will know, a new appearance here is merely a special incentive to trial. My African birds, though not hungry, attacked with the greatest zest various Oriental and South American butterflies that I showed them—some of them of highly nauseous species, and all representing appearances that they had never seen before. Similarly, to an egg-eater an egg is recognizable as such whatever its coloration. If the pattern be new, so much the worse for the egg. A Monitor that came into the possession of my friend Mr. T. Honey, the energetic Curator of the Lourenço Marques Gardens, refused raw beef until forcible feeding with it showed it that it was a suitable food, but from the first it readily attacked fowls' eggs, though it had probably never met with them before. A lemur that I captured in the thick of the Jihu jungle, far from any human habitation, and to which I offered an unbroken hen's egg that very day, did the same. In the same way the rat, the lemur, and the

mongoose of my experiments were eager to try, and did try, every kind of egg offered them. It was only after trial—smelling, tasting, or commencing to eat—that their refusals took place. Moreover, the eggs were nearly always offered *opened* and the opened portion brought right up to the animal's nose before being deposited just below it.

I have gone into this criticism, though it was obviously (through my own fault) based on a misunderstanding of what took place in the experiments and a non-realization of the care with which they were conducted, because I find that it impressed a good many of those who heard it. Applied to the trial of Palearctic eggs on an Indian mongoose there is more to be said for it. I was myself much disappointed at having, in the end, to use that animal. But I was anxious to experiment on something further, if only for my own satisfaction, and, apart from the knowledge that I would be using eggs of genera that also occur in India, I realized from my general experimental experience that the animal's use was in reality less objectionable than at first sight it might appear. Most animals are specialized in some particular direction: some prefer Diptera, some Orthoptera, some are browsers, others grazers; yet within each large class of prey there is, despite individual differences, a wonderful *tendency* to sameness in the preferences of animals generally, even when (as often happens) they stray somewhat outside their own special sphere. In the same way imported herbivorous animals in Africa show very similar preferences to those of African Antelopes, and domestic fowls and northern migrants to those of indigenous insectivorous birds. A cat, a wild raven, and a lion showed the same preference with regard to prey which could only be regarded as the natural food of the lion. A domestic cat's preferences in birds were very similar to those of an African lemur (the lemur of the egg-experiments), and a Woodford's Owl on which I experimented confirmed in the greatest detail the butterfly-preferences of my diurnal birds, migratory and otherwise. It all shows (and I could adduce yet better evidence of the fact) that it is no pure matter of taste—

of mere capricious likes and dislikes,—but one of intrinsic difficulty of digestion, felt in greater or less degree by all enemies alike.

It matters little, in any case, whether my mongoose's preferences were, or were not, those that would have been shown by an English weasel or magpie. The important point is that he showed preference in eggs at all. Every animal I have experimented on—mammal, bird or reptile, vertebrate or invertebrate—has shown these preferences, whether the prey were plants, seeds, mammals, birds, worms, snails, insects and their larvæ, or insects' eggs. Is it likely that birds' eggs are alone exempt from so general a rule?

Arguments from analogy are frequently fallacious, and I have used many such in the last few pages; yet they are apt to be highly suggestive, and what they suggest in the present instance seems to me to be that preference in the eggs of birds is, at any rate, worth approaching with an open mind.

I will only add:—

5. *My own Criticism.*—It is, that a wild animal, having more abundant exercise, will develop a more ravenous appetite than a captive animal. I had the opportunity of testing this possibility on my wild insectivorous birds, and I found that they probably did become hungry enough to eat highly nauseous prey more frequently and easily than birds in confinement. Yet it amounted to very little. Even the wild birds soon discarded *Acræinæ*, &c., and eliminated grade after grade from their *menu* as they gradually satisfied their hunger. It would have been the same, I imagine, for my egg-eating mammals had they been in the wild state: a mere postponement of first rejection, accompanied, it might be, by a compensating postponement of final repletion. But it is on this rock, if on any, that my experiments may split.

It is also true (another criticism) that I judged that neither rat nor mongoose placed any egg at all so low as the latter placed a Burnet moth, or as either might have placed an *Acræa*, a *Mylabris*, an adult Drongo, or a Wood-Hoopoe. It may have been that, using so few species of

eggs, I did not happen to hit on the unpleasantest grades. Or it may not. In either case the principle of graded preference—of progressive elimination—remains, and this is all that is necessary for our purpose. Actually I should say that their lowest-placed eggs were to the mongoose and rat about what *Mylothris* and *Belenois* are to insectivorous birds. Both genera are, at any rate, so well protected as to possess many mimics.

IN FAVOUR OF PREFERENCE.

The remarks of two, I think, of the speakers at the meeting suggested strongly that preferences *are*, perhaps, sometimes seen in the field—the special search, for example, of certain of the British Corvidæ for particular eggs; and an interesting question, and one that might perhaps be fairly easily answered, is: Do any of the Corvidæ, as a regular practice, search thus for relatively well-concealed eggs, as those of plovers and game-birds, while conspicuous nests in the same neighbourhood remain for the time being untouched? If this were found to happen, the observation would, at any rate, be suggestive, even if the contents of some of the conspicuous nests were also eventually to fall a prey.

I have already referred to the different flavour and consistency of each of the few eggs that we ourselves most commonly use for food. Mrs. A. L. Selater, who was staying with us at the time of my rat-experiments in 1913, told me then that, as a girl, she, with her brothers, used sometimes to eat birds' eggs, and that they learned to avoid one common egg, she had forgotten whether Thrush or Blackbird, owing to its unpleasant taste. It was, therefore, with the greatest interest that I read the following passage in one of two letters, full of information, which Mr. H. M. Wallis was so kind as to write me on April 15th and 26th, respectively, after being present at the discussion on the subject: "Relative palatability of eggs. I have in all cases of difficulty sucked eggs of any value rather than trust to the blow-pipe, and have found

the flavours vary immensely. Thus, Robin, Nightingale, and Swallow are beastly. But the white eggs of the Little Bittern are as sweet and mild as cream, nor are the eggs of the Barn-Owl much inferior to them." And in his second letter he refers to the well-known strong odour of Petrels' eggs—"but, is it deterrent?"

If Petrels' eggs are by any chance of low-grade edibility—and this, in the last resort, can only be ascertained by experiment, as Mr. Wallis actually suggests it should be—I would imagine that the smell is likely to be useful for aiding in their recognition by enemies rather than deterrent in itself; just as many of the smells of insects are probably mnemonic, like their appearance, rather than directly deterrent. The real deterrent quality is usually something more deep-seated than appearance, smell, or taste, but differences in it, both of degree and kind, are commonly accompanied by differences, strong or slight, of taste and (to other mammals than man) smell; and it is on this account that the observations I have quoted are exceedingly interesting and suggestive. They amplify greatly the common knowledge that eggs vary in flavour, and extend it to raw eggs. It does not necessarily follow, of course, that flavours and smells that are agreeable to us are always associated with great digestibility in relation to natural enemies. *Danaïda chrysippus*, one of the most nauseous of butterflies in its effects, has a mild and not unpleasant nutty flavour, while members of the unpleasant genus *Mylothris* smell sweetly of menthol and sweet-briar. Nor does it follow that an object which we find wholesome when cooked is necessarily as digestible to its other enemies when raw. *Monticola* is greatly disliked by my cat, which refuses to eat it even when specially starved. Yet, toasted through (feathers and all), he has readily eaten it to repletion-point.

Mr. Wallis goes on: "Although the Little Bittern lays in an uncovered, or slightly covered, nest, I have not chanced on any sucked eggs, whilst the covered nest of the Water-Rail is, in my experience, exceedingly liable to be raided by

rat and weasel." The case is not a good one, as the observations on the Little Bittern were carried out in a locality in which rats were not actually noted, though snakes were abundant ("seven asleep on one raft of reeds"), but it is useful as indicating a line of observation which may give interesting results.

He further suggests problems that, as he rightly insists, are probably explicable only in relation to a number of interacting factors, of which, however, varying degrees of unpleasantness in the egg might well be one—problems of distribution and relative success. Also, he rightly attaches much importance to the great principle of compensation, and naturally at once sees what a straightener-out of our difficulties the acceptance of nauseousness as the hitherto missing counteragent to conspicuousness in eggs would prove to be. He expects the eggs of the Nightjar and the Stone-Curlew "to be fairly edible," being protected by their own coloration and that of their parents, but thinks it likely that the egg of the Song-Thrush, a bird "not so pugnacious as a Blackbird and much less so than a Mistle-Thrush, and *far* less than the Fieldfare at the nest," will be "refused by birds and animals which would take the egg of Blackbird and Mistle-Thrush." And he mentions a great Italian marsh on which the Water-Rail (covered nest) and Baillon's Crake (open nest, "or rather tiny pad," and protectively coloured egg) were found breeding successfully. But what of the Little Bittern, with a white egg and open nest, yet "abundant" there and "enjoying a large measure of immunity"? The Bittern's sharp bill occurs to one, yet cases could be given in which there is no such escape as this from the conclusion that there is a missing counteragent.

I would suggest, finally, that the common habit possessed by birds of removing or deserting eggs or young that have been visited is surely essentially connected with the possibility of deferred attack by an enemy that was not hungry enough for them on first discovery.

SUMMARY OF THE POSITION AS REGARDS PREFERENCES.

If graded preference is found to be at all general here, it will provide us with a fairly complete and satisfactory explanation—at all events from a purely selectionist point of view—of the coloration of the eggs of birds, and much that has hitherto seemed difficult will be explained. On this account, the possibility is worth considering.

That there is a basis for possible preference in the varying composition of the contents of different eggs is suggested by their varying taste and consistency. That the former should be in some cases unpleasant to the human palate is highly suggestive, though not conclusive. A consideration of this kind (the “peculiar smell” of *Heliconidæ* and *Euplocinæ*, and the former’s possession of exsertible glands) constituted the whole of the more direct evidence on which Bates founded his theory of mimicry, now well supported by evidence and widely accepted. But, for eggs, we have in addition the evidence of a number of experiments, apparently reliable so far as they go. Does this evidence represent what occurs amongst egg-eaters generally?

The critic’s position is that, while there is nothing inherently improbable in the idea of preference, he sees no signs of it in nature*. The fairness of this may readily be admitted. But (since uncontrolled acceptances prove nothing) neither has any good evidence as yet been adduced against preference. Proof or disproof remains, therefore, a matter for special observation.

THE CLAIMS, AND A DEFINITION.

The claims made are worth re-stating briefly to avoid misunderstanding. It is not claimed that some eggs are not eaten. *All* are eaten, even with eagerness, under certain circumstances, though some are believed to be refused more frequently than others. Nor is it claimed that all egg-eaters necessarily thus discriminate, though, for the support of the theory, it would be necessary for a

* Rev. F. C. R. Jourdain, in a letter (17. iv. '15).

considerable proportion of them to do so. Nor, again, is it suggested that either colour, smell, or (necessarily) taste are in themselves protective. The real protection, causing occasional or frequent refusal (according to its strength), is believed to be indigestibility in varying degree, which can be overcome by sufficient gastric activity such as is present especially in an empty stomach, and greater in a half-filled stomach than a full one. Coloration and smell would be of use merely to enable the enemy to recognise, without breaking it, an egg, already known to him, that he is not at the moment hungry enough to digest, and the sight or smell of which, therefore, is sufficient to produce in him a feeling of disinclination.

Mimicry is worth defining briefly again in the sense in which I shall refer to it below—not that I lay excessive stress on its occurrence. It is the resemblance (brought about by the selection of the appropriate variations, large or small, “mutations” or “fluctuations”) of an abundant and more or less deterrent species (the “model”) by a species more liable to attack (the mimic). The latter’s greater liability to attack may result from a smaller power to deter (whether by indigestibility or otherwise), or from being less well known to enemies, and so more liable to suffer from *mistaken* attack; or from a combination of these relative disadvantages. It is even conceivable that points of resemblance occurring as between two equally deterrent and abundant species might be selected owing to the doubled reminding-power afforded by the combined populations and the facilitated task for the memory provided by recognition characters in common. A “mimetic association” is the colour-group formed by a model (more or less indigestible or otherwise deterrent) and its various mimics, whether these have mimicked it for increased notoriety* (being

* Not really Müllerian mimicry, though the basis is still mainly population. Müller’s view was not “more reminders, simplified recognition, and less mistaken attack,” but “equal destruction (by young enemies) whatever the population,” the greater population thus losing a smaller percentage. The first view seems the more probable and is supported by my experiments.

deterrent in themselves) or for protection from legitimate attack. Or the model round which the others, so to speak, centre, may be multiple—consisting of several related species of nearly the same appearance. It is in this sense that I suggest below that the Tits' eggs may have been the model for one association and those of the *Picariæ* for another.

An illustration will be useful. My cat was once completely nauseated by a Drongo I gave him, and thereafter "placed" Drongo very low indeed. One day I offered him, first a Drongo, then, in turn, a male Cuckoo-Shrike (*Campephaga nigra*), a Black Flycatcher (*Bradypornis ater*), and a Black Tit (*Parus niger*). I laid each on its back on the ground, in which position all, the first three especially, resembled the Drongo. The cat refused the Drongo, and thereafter refused even to come forward and smell any of the others. I now turned each one in turn on to its breast. Each was still neglected till I came to the Tit. This the cat at once came forward to, the white of the upper wing-coverts obviously showing him that it was no Drongo. I now carried out a preference experiment with meat-scrap from each bird. I found that the Flycatcher was placed nearly or quite as low as the Drongo, the Cuckoo-Shrike far higher, yet by no means amongst the species that are accepted to reptation-point. Thus (if it be a case of mimicry—as field-observation suggests), the association, as we find it at Chirinda, consists of: (1) two species of Drongo, abundant and low-grade, constituting the "model"; (2) a Flycatcher, which, being as low-grade as the Drongos, yet much scarcer, might be regarded as having mimicked them for the sake of greater notoriety; (3) a male Cuckoo-Shrike, scarcer, also higher in grade, though still to some extent deterrent, and probably, therefore, a mimic in virtue of its greater liability to both legitimate and mistaken attacks.

THEORY.

1. *The Defences of Eggs.*—The principle of alternative defences and complementation that underlies Wallace's explanation holds good. Some eggs are guarded by more

or less formidable or pugnacious parents, perhaps prompt sitters, others have close-sitting parents with concealing coloration, others again are covered in (whether in a hole, a domed or deep nest, or the interior of a dense thicket)—or covered merely when left; and it is these and other counteragents, as we may call them, to conspicuousness that, separately or in combination, have enabled them to develop or retain the latter quality in their coloration—white or spotted, or vivid blue, or (like Barratt's Bulbul) a glorious pink—and so on; a conspicuousness that, without the counteragent, might have rendered them liable to detection from some little distance.

Against these conspicuously-coloured eggs we must place those which, lacking counteragents to conspicuousness, and liable themselves to be first seen were they conspicuous, are, instead, protectively coloured—as those of Plovers.

So far, this is Wallace's explanation, but with the coloured conspicuous eggs added to the yet more conspicuous white. It explains the procryptic element in those eggs in which that element is present, and it explains how the others can afford to be conspicuous. It does not explain the latter's coloration. Nor does it explain all cases of relative conspicuousness in nests.

Missing counteragents* may help to explain some of these cases. But the great missing counteragent, capable of aiding heavily in the explanation of such cases—and of many others—is likely to be some degree of indigestibility (or "nauseousness," or "unpalatability") in the egg itself. That some degree of indigestibility (it need not be of the most marked order if other counteragents are present to complement it) may be the partial explanation of, for example, the survival of the conspicuously-laid white eggs of some Colies and Doves, and of the often very fairly conspicuous nests of Buleuls, Shrikes, &c., was suggested by my experimental results.

* Of these, fecundity and perseverance in face of persecution may be one, hardness of shell in relation to certain enemies another, out-balancing advantages at another stage (as of food and "mentality"—*Wallis*) a third.

2. *Diversity and Distinctiveness*, also the *Tendency* to Uniformity within the Species or Form*.—Should it be found not merely that nauseousness exists, but that there is a gradation between some species of eggs that are only eaten through hunger and others that an individual enemy will eat to repletion-point, we may conclude that the need for distinguishability from pleasanter forms (parent and otherwise) is, and has been, widespread, and we shall have at least a contributory explanation for the qualities italicised above. Probably, in many cases, somewhat more than a merely contributory explanation—for inter-recognition between eggs is out of the question, and necessity for recognition by parents is probably urgent only in those species (numerous enough) that may be victimized by Cuckoos, though just possibly present (as Mr. G. L. Bates suggests) in birds that build in close colonies, where, however, it would encourage variability.

The necessity for differentiation from less deterrent parent-forms might well have been of much importance, for, unaccompanied by some distinguishing mark, a variation in the direction of greater nauseousness is unlikely to be actually selected. The selection of the curiously netted chalk layer in the egg of the Guira Cuckoo and of much else that is striking and peculiar in eggs (and in animals generally) could be in part accounted for in this way; while the oft-repeated necessity for differentiation from successive parent-forms that might accompany a very gradual or much interrupted increase in indigestibility might conceivably sometimes produce the utmost heights of distinctiveness. Whether such variability as we find in the eggs of the Guillemot will be explained as due merely to the absence of the necessity for recognition by enemies (whether through present high acceptability or the fact that an enormous annual colony and the qualities of its eggs, irrespective of coloration, will be a matter of the utmost notoriety to the

* I use the word advisedly, for such a "tendency" actually exists, in spite of the great variability of many eggs—a variability that I believe to be perfectly explicable.

enemies from far and near that will flock to it daily when hungry enough) or to a need for recognition by parents, or to both, is a problem to be solved by special observation. To a case of variability that I have myself begun to investigate (namely, Weavers' eggs) I will refer later.

Another factor contributing to diversity (within or as between species) would doubtless be Wallace's—of pro-cryptic adaptation in varying directions, often from bases already different. It would apply not only to those eggs the coloration of which does definitely contain a pro-cryptic element at present, but, indirectly, to eggs formerly in different ways pro-cryptic but now brightened through having become possessed of a counteragent to conspicuousness (*cf.* Darwin on caterpillars, *Descent of Man*, 2nd ed. p. 501*).

3. *Conspicuousness.*—Given the existence of nauseousness, conspicuousness would be useful in relation to the mistaken attacks of enemies through the assistance it would give to recollection and recognition, and its selection might be brought about even in a but slightly deterrent species either in this connection or through any other factor making for conspicuousness whenever a suitable counteragent already existed or was developed *pari passu* with it. Where the egg is concealed up to the moment at which the enemy looks into the nest, its appearance might be usefully regarded as a vivid last appeal to the enemy's memory, the distinctive nest-appearance being the first—a suggestion as to why the habit of building true to type might have been selected. And the very fragility of eggs must render their need the greater for mnemonic coloration of a particularly memorable kind, and must aid in its effective selection (*cf.* Darwin, *loc. cit.* p. 499).

* This point, with the additional counteragents suggested in a previous footnote, the view that any variation in the direction either of variability or conspicuousness will survive provided a probable counteragent is forthcoming, and the influence of cuckoos towards both distinctiveness and (especially) polymorphism in the eggs of their hosts may seem to some to constitute, without nauseousness, a sufficient explanation of the coloration of eggs. Actually, all this fails to account completely for the facts.

It will not follow that equally conspicuous eggs are equally nauseous, or *vice versa*. A good counteragent might enable the highest conspicuousness to be selected in a but slightly deterrent egg, while a far more deterrent egg without other counteragents, yet insufficiently deterrent to make up entirely for their absence, might have to be to some extent concealingly coloured.

4. *Colour-groups*.—In spite of much general diversity, we find that a number of the eggs of a given area tend to fall into definite colour-groups. If the suggestion that nauseousness is present in eggs be correct, it is possible that occasionally a colour-group may be to an appreciable extent in the nature of such a mimetic association as I have defined above. The model for one such association (white with pink spots, occurring mainly in holes and domed nests) might be in Europe the eggs of the Tits. My mongoose showed a dislike for those of *Parus major*. The model for another group, which also figures strongly in holes, might conceivably be provided by the eggs of Picarian birds, most of which are white and are laid in holes. I have no actual evidence here, except for the eggs of *Colius striatus*, placed low by my rat. Adult Woodpeckers of three genera were placed very low by my animals*.

The fact that white eggs in holes are a *strong* group might be accounted for sufficiently by the fact that some powerful families that tend to lay white eggs whether they nest in holes or not (as Picarian birds and Owls) do, actually, lay most often in them. Omit such cases (in which whiteness is probably now mainly a matter of affinity, though the laying in holes may have been, in its origin, either a cause or a result of the whiteness and synapomorphic advantage may also sometimes now be present) and relatively little is left to account for. Mimicry may partly account for the white of some of the unrelated members of the group, and an additional explanation for the colouring of

* That a Woodpecker possesses fighting-weight must not, however, be overlooked. Mr. Wallis mentions the case of a squirrel found dead by a friend of his in a Woodpecker's hole, with its skull split.

the models could be found (if necessary) in the suitability of white as a warning colour for dark places. It is the warning colour *par excellence* of night-flying Lepidoptera. And Mr. Pycraft has suggested that white in holes, for the same reason of visibility, is useful for the avoidance of accidental breakage by parents*, and, it might be added, by other animals sheltering in burrows. Last, and not least, we may add to these various possible contributing factors (as an alternative or crown to variability) the loss of pigment when it becomes useless and unselected, as in an egg that is now inaccessible (through position or an effective guard) or in darkness.

5. *A Reservation.*—The possibility of mimicry in eggs must be treated with caution, as pure coincidence in their coloration is so general a phenomenon. As I said at the meeting: “The coloration and pattern of eggs is so simple as to lead us to expect the same scheme of colouring to crop up over and over again quite independently of advantage. I have lately been working at eggs in the British Museum and at Tring, and nothing has struck me more than the fact that this continually occurs—very often, it is true, obviously through affinity, but very often again not. And this state of affairs warns us to be very wary about attributing a given resemblance to mimicry.”

In support of this warning, I specially exhibited several African eggs that in appearance are indistinguishable from certain unrelated English eggs. It matters little whether we call such accidental resemblance “coincidence” or the result of “parallel evolution.”

“At the same time,” I went on, “it is a state of affairs under which mimicry may often have taken place—for what is mimicry, at best, but *selected* coincidence?—and the material for selection, the coincidences, are here abundant. So that if we rigidly confine ourselves to a few highly

* Believed by a speaker at the meeting to have been suggested originally by Seebohm, but Mr. Pycraft tells me that, so far as he is aware (and he has looked up that author), the suggestion originated with himself.

probable cases a study of resemblances in birds' eggs may help us a little to understand their coloration." The two examples actually suggested above are intended rather to illustrate a possibly useful line of contributory explanation than to be regarded as put forward with any real feeling of confidence in their individual validity.

6. *Parasitic Cuckoos' Eggs*.—Mr. Stuart Baker, whose field experience in this matter is probably quite unrivalled, considers that it amply supports the theory of Dr. Baldamus. I have myself, in the past, been somewhat sceptical of the part therein implied to have been played by the foster-parent in eliminating Cuckoos' eggs unlike her own; this is in view of the fact that as a schoolboy I sometimes replaced an egg I required with another of quite different appearance, or even with a rounded stone, and the old bird would go on sitting. Mathews ('Birds of Australia') quotes an instance in which Petrels were found still sitting on their empty nests a week after the removal of the eggs. But, if we regard the tendency to reject suspicious-looking eggs as selection's natural reply to special victimization by Cuckoos, this "readiness to sit on anything" may have meant no more than that the species tested had not been greatly victimized. Under these circumstances, mimicry in Cuckoos' eggs might well, after all, often have been brought about by the action of the host alone. The finding of deserted nests containing a Cuckoo's egg certainly seems to support this view, but the question must still, I think, be asked: "Was it detection of the Cuckoo's egg that caused the desertion?" At any rate, the part played by the foster-parent in the elimination of unconvincing substitutes can be very easily tested by experimentation on wild birds.

In any case, whenever the foster-parents' eggs were more or less low-grade, the discriminative action of enemies might well *also* have come into play, and have contributed to the selection of the resemblance. An egg, little known (or known to be pleasanter), and unlike the others in the nest, would be quite liable to special testing even where these

were known and unacceptable—unless, indeed, it resembled some other well-known egg that was then unacceptable. It is just interesting in this connection to recall the fact that the eggs of the English Cuckoo, even when laid in other nests, most commonly resemble the eggs of Wagtails, Pipits, and some Warblers, and to note that the eggs of Wagtails, Pipits, and, at any rate, some Warblers were not placed very high by my animals, the Pied Wagtail's in particular—not that my mongoose's preferences were necessarily the same as those of English egg-eaters.

7. *Polymorphic Eggs of Weavers.*—I refer especially to members of the genus *Hyphantornis*. Each species lays several different types of egg. The types are well marked and constant, and intermediate forms are relatively rare. Apparently each hen-bird lays only one type. Nearly every form resembles more or less strongly some type of unrelated egg occurring commonly in the same area. The figures in Plate XIX. illustrate this point.

Mr. G. L. Bates's suggestion ('Ibis,' Oct. 1911, p. 585) that the distinct types of eggs "must aid each hen-bird in finding her own, to the benefit of the race," might account for the distinct types, but not for the resemblances. In any case, we meet with a similar phenomenon in the eggs of many solitarily-nesting Warblers (*Apalis*, *Cisticola*, *Prinia*, etc.) to which the suggestion could not apply. I may, of course, be unintentionally exaggerating the resemblances. I think not. And, if not, I am rather tempted to think that we may have here a case of polymorphic mimicry such as occurs in insects in the females of *Papilio dardanus*, though probably with a few larger synaposematic elements in the mimicry.

There is a good deal to be said for the view. I will hold this over till a future occasion, when I hope to discuss the whole problem in some detail. There are also two or three quite strong objections to it—resemblances less good or absent in at least one of the species (and in the Warblers), darkness of some of the nests, characteristic appearance of the nests,

a good differentiating character: my view that distinctiveness in nests generally is quite largely for recognition by enemies, is at first sight in contradiction with the suggestion of mimicry between eggs in unlike nests. I showed at the B. O. C. meeting that these objections are not insuperable. Either synaposematism or the view that the nest-appearance is only a first line of defence, and the egg-coloration a last resort, will meet the third of them; while it is not necessary to suppose that polymorphism even here is purely or in its origin a matter of mimicry, or that the mimicry when it arose was necessarily at first perfect.

8. *Darkness of certain nests*, which nevertheless contain coloured eggs, is an objection to any view that regards the coloration of eggs as a visual appeal. I judge from my own special observations, however, that the darkness is seldom absolute; and it must be remembered that an enemy, unable to digest certain eggs or disliking their taste, and relying on sight for their recognition, may even try not to block out all light. So far as nestlings' mouths are concerned, these are usually at once directed, on craning neck, towards or *through* the opening. This is true even of birds that have the opening in their nests below.

9. *Recognition by scent an objection*.—I have constantly known mammals (including my eaters of eggs) that rely very much on scent for recognition, satisfied with mere appearance, and deterred thereby from smelling. It would even seem to be the *rule*, once the appearance has been well learnt and while it is well remembered, and the smelling of such eggs that occurred in my experiments was often the result of pressure on my part. I have even known such animals mistrust the evidence of their noses when it seemed to conflict with that of their eyes, though this is probably quite unusual. There can be no doubt that they must be regarded as a serious factor in the matter of coloration, even when we have excluded all that are exclusively nocturnal, and allowed for the fact that the olfactory appeal will often succeed where the visual appeal has failed. At the same time I regard it as one of the stronger objections

to the experiments I am about to describe that they were confined to animals that rely greatly on scent, and are, therefore, a less important potential factor in the selection of recognition-coloration than are animals that have to rely on sight alone.

I might say in conclusion that I have already, in the course of my work, had to throw aside or modify so many tentative explanations for various facts, that I fully expect that much that I have written in this paper will yet meet the same fate at my own hands or that of my critics. Theories are the stepping-stones to knowledge. But not when we refuse to leave them behind us. I shall consider my present suggestions to have amply served their turn if, discarded themselves, they should nevertheless have resulted in an awakened and resultful interest in the explanation of two of the most fascinating and neglected of colour-problems.

SOME FURTHER OBSERVATIONS AND REFLECTIONS.

Since I wrote the above paper I have had a limited opportunity for further observation and experiment. I will touch briefly on a few of the more interesting results, reserving a fuller account for a future occasion.

The selective factors in the matter of Cuckoos' eggs.—I have placed eggs not their own in the nests of a number of birds and watched the result. The first three or four, although contrasting strongly with the bird's own eggs, were accepted, and I expected a repetition of what I remembered as my boyish experience. Subsequently, though many acceptances still occurred, the majority of the changelings were rejected, and Prof. Newton's explanation of the facts with regard to the eggs of the English Cuckoo—"That certain kinds of birds resent interference with their nests much less than others . . . but with other species it may be, nay, doubtless it is, different"—was supported. I am delighted to have obtained so unequivocal a result in favour of Mr. Stuart Baker's view on a point on which I was inclined to differ from him; and I am glad to have indicated, at my own

expense, the value of definite experiment as against uncontrolled stray observation. Above all it has been fascinating again to watch natural selection at work.

The result by no means affects the general explanation of the distinctive element in the coloration of eggs as being for recognition by enemies, unless it should be considered that parasitism was once so rampant that distinctive coloration had to be developed in order to enable parents to distinguish their own eggs from those of Cuckoos that were following them up in the matter of coloration. This would be an alternative, if not very probable, explanation, and it may certainly have acted as an important contributory factor in a number of cases—in some of them towards the selection of high distinctiveness, in others towards polymorphism (as in Warblers and Weavers). Polymorphism in the host's eggs would certainly reduce the individual Cuckoo's chances of matching its egg, if (as seems likely) its choice is based on recognition of foster parent and nest; and I do not know at present that polymorphism occurs in this definite form outside of the birds that Cuckoos victimize. The variability of the Guillemot's egg is rather a different thing, and will doubtless be found to possess a special explanation of its own. The explanation of the resemblances remains unaffected.

Nor is the view that the attacks of enemies may have contributed to mimicry in Cuckoo's eggs disproved, though it is certainly rendered unnecessary and, at best, secondary. Where the difference between the eggs exchanged was slight no rejection took place, but I do not lay stress on this. A case I shall refer to below suggests that further experiment might have produced occasional cases of finer selection.

“*Darkness of the nests*” argument.—In the above-mentioned experiments *Hyphantornis jamesoni* regularly ejected eggs not its own, and a *Sitagra ocellaria* an egg of *Hyphantornis nigriceps* of the spotted blue type. Still, neither's nest can be regarded as dark. But the *H. nigriceps* also ejected the *Sitagra* egg that was used in the above exchange. This is highly important, for this *Hyphantornis* builds, at

Chirinda, the darkest weaver nest I know—really very dark ; and not only was there little difference in size, shape, and feel between the eggs, but there was also no great contrast in their coloration.

Mr. Bates's suggestion that the different forms of Weaver's eggs are for recognition by the parents.—In three cases I made a complete exchange of eggs between contiguous nests. In each case, instead of exchanging nests, the birds deserted. I have also, both now and in the past, noticed excitement on the part of a particular bird or pair of birds as I have tackled each particular nest, showing that the birds know their nests even at a little distance by their position, etc. More observation is wanted nevertheless, especially of all the causes of the squabbles that take place in a large Weaver colony.

Unpleasantness in eggs and nestlings *.—I have commenced to experiment on myself with eggs, and I can already confirm to some extent Mrs. Selater's and Mr. Wallis's statements as to their different tastes : their different "strengths" would be almost better. It is wonderful, nevertheless, how similar the most unrelated eggs may be in taste, and the differences I have noticed up to the present are merely comparable to, yet greater than, those that obtain as between different genera of Nymphaline butterflies which are nevertheless divided up into numerous grades by their enemies. However, I have not yet tried any eggs that were placed at all low by my animals. I have also found, I think, that some eggs are more or less nauseating when swallowed, while others are not : not that what nauseates myself will necessarily nauseate a Crow. In any case the experiments have not yet proceeded far. I am waiting for a bird of the Crow family in order to continue my main experiments.

I have added slightly to the list of nestlings disliked by my cat, and have noticed in three of them the unpleasant smell described by Mandina in a conversation I have quoted above. The worst was that of *Bycanistes cristatus*—so

* Yet further testings enable me to confirm Mr. Wallis more completely.

pungent and nauseating that we had to banish the young birds from the verandah. The cat refused one when hungry, though he eats the full-grown bird practically to repletion; but the smell may, of course, disappear with death.

Nestling distinctiveness in relation to recognition by parents.—I have referred in footnotes to my experiments in this connection. That the distinctive element in the call-notes of nestlings may be of use to parents has struck me lately in thinking over the numerous escapes of young birds that, as I have myself seen in relation to snakes, occur through their fluttering down from the nest. Their calls certainly take their parents to them (as I have often seen), while those of another species presumably would not; yet, to account for the selection of distinctiveness in this connection, one would have to imagine that it is a common occurrence for nestlings of more than one species to be out of their nests together. The solicitude shown by the parents for these strayed nestlings (and for caged nestlings) makes one wonder at their alleged ready desertion of those that are ejected by Cuckoos.

Resemblance between mouths of Cuckoo and foster-parent's nestlings; ejection of fellow-nestlings.—A very young Cuckoo nestling in a Bishop-bird's nest had the mouth a rather dusky orange, and different, therefore, from the rose-coloured mouth of its surviving fellow-nestling. This, and doubtless numerous other cases, must stand against my suggestion made early in this paper. At the same time the orange was turning to salmon (especially under excitement) before the bird's death, a few days later. A fledged Didric Cuckoo, now in my possession, had a glorious mouth when taken from the nest of its *Hyphantornis* foster-parents—an exaggerated weaver-red, with the pale portions corresponding with those of a weaver's mouth. A rush of blood reinforces the pigment, for when the mouth was forcibly opened it was paler, and showed a tell-tale Picarian tongue. Both the Cuckoos had the Weaver's note, "tsip, tsip," and even more than the usual *Hyphantornis* head-waggle. It would be interesting to know whether these characteristics

are also possessed (as they may be) by Cuckoos that victimize chiefly other birds than Weavers.

The younger Cuckoo (I have not identified it) gave me demonstration after demonstration of the gentle art of evicting fellow-boarders of various kinds from even quite deep nests, and, incidentally, of the use of the highly prehensile feet in preventing himself from following them (as he invariably did when he pushed them from the smooth surface of my hand). The act of eviction is not a simple hoist. There are many co-ordinated movements and an exhibition of tenacity that may continue for ten minutes or more, and that, through all the rests and demands for food that punctuate a difficult operation, refuses, like a ratchet-worked stump-lifter, to yield one millimetre of height gained. The case is of much interest for its bearing on the question of the origin of adaptations. It is impossible to believe that the habit in its present complexity arose as a single variation. If it did not, it is just as impossible to believe that in its early stages it could have been selected—at any rate in the newly-hatched bird; for a miss is in this matter as good as a mile, and there would have been nothing at all but misses. One must invoke either the Lamarckian explanation pure and simple, or (2) the supposition that the habit was first selected in flat nests only (and this is insufficient), or (3) suppose that it arose and was first selected in nearly full-fledged birds and has passed back into an earlier stage in development, being gradually perfected as it did so—an interesting possible instance of the origin of an instinct from, probably, a partly deliberate act. My present Cuckoo was *farouche* in every sense of the word when I took it, full-fledged, from the nest. It threatened and attacked myself with mouth displayed after the manner of an adult at bay. It tolerated companions in the nest only so long as they remained still. When they fidgeted or began to climb on to itself it did not, like the younger Cuckoo, push under them, drop its head, extend its legs, procure successive purchases for its feet, and purposefully heave and hoist; but it showed irritability and sharply pushed or buffeted

them with its wings, and it may be that it was in some simple action like this that, as I have suggested, the whole instinct and action of ejection originated. I will discuss the experiments more fully in a more appropriate place.

Are Tongue-spots a Nestling Adaptation?—I scoured two nestlings of *Dryoscopus guttatus*, so fully fledged that the male flew from the nest on my approach and was only captured with a little difficulty. They still had the perfectly plain orange-yellow mouth. Nearly three weeks later, when they were well able to fly, they were commencing to show the twin spots, and a fortnight later those of the male were very pronounced, the mouths being otherwise still orange-yellow. A fortnight or so later, the female was at the stage then reached by the male, with a mouth equivalent to the nestling mouth of, say, *Prinia mystacea* or *Laniarius sulphureipectus*. The male had advanced further, through a stage which one often finds represented in nestlings of *Cisticola natalensis*—tongue and inside of mouth flesh-coloured, submarginal parts still yellow—through an all-pink stage (with twin spots) that occurs in other nestlings of the same *Cisticola*, as well as in other warblers, and that, without the twin spots, would be like the adult mouth of *Lanius collaris*, to a stage in which an incipient darkening of the apical portions of the mandibles produces a resemblance to the mouth of several adult birds—*Batis molitor* and *B. erythrophthalma*, *Graucalus pectoralis* and *cæsius*, *Podiceps capensis*, etc. The final stage, as we know, will be all black.

Of course it may be argued that if the twin spots were the last dark colour to disappear, they may be the first to appear again with the re-darkening of the mouth, and that, though a nestling adaptation, they have had in this instance to give way for a time to a pattern which, under the species' present circumstances, offers it greater advantages—perhaps enabling the young to be mentally associated by enemies with those of *Lanius collaris*, which the female *Dryoscopus* nestling rather strongly resembled. Much further work is needed, including observation of embryonic tongues within

a day or two of hatching. Meanwhile, I will perhaps not be blamed too greatly for provisionally placing this mouth and that of *Cisticola erythropus* amongst the arguments against the nestling-adaptation view. I may add that an unhatched *Prinia* had the spots quite separate and unconnected—which leads one to enquire whether the tongues shown in my text-figure were not perhaps specially advanced rather than reversionary—and that a younger embryo of *Heliolais*, the mother of which had not lost the twin spots, had its mouth already tinged with yellow, but (so far as I could see) no spots. Those *Prinia* embryos nearly as advanced showed no spots, but I am not sure that they were yet beginning to show any pigmentation at all.

I have already, in a footnote, referred to the fact that the substitution of a nestling with a spotless mouth for one possessing the twin spots strongly developed, did not to all appearance result in any detriment to the former or in trouble to the latter's parent. I have also specially tested the rest of Mr. Pycraft's view, that mouth-spots "occur just in those areas where the mouth is most sensitive to touch, so that they serve a double purpose—they form a guide to the parent, and ensure a mechanical closing of the mouth directly the right stimulus, given by the touch of solid food, is administered." Mr. Pycraft applies this view even to nestlings "hatched in open nests, on the ground, amid short grass," believing that the spots "were probably developed before the birds adopted this more open nesting-site; and, this being so, . . . they are still needed to serve as a cue, so to speak, to the right co-ordination of movements necessary for the sure transference of food to its destination."

The view may quite likely apply in its entirety to cases I have not tested. I have experimented on very many nestlings, however, mostly with the twin-spot tongue and in covered nests, with the following general result:—(1) the apical portions of the mouth, including the tip of the tongue, are less sensitive than the inner portions. Mouth-spots occur in both areas. (2) Of the more sensitive parts,

the back of the tongue and the palate both quite commonly failed to respond to stimuli that tickled my face, but were not felt between my knuckles. Yet the same stimulus applied to the gullet (the tongue not being touched) often led to swallowing. (3) The back of the tongue often failed to respond to faintly stronger stimuli that produced swallowing if applied to the palate. This was noted in *Prinia* and three species of *Cisticola*, and verified by experiment after experiment. Sometimes a light object was left lying on the spots, or a small grasshopper tegmen, or piece of chitinous flesh was rubbed back and forth on them, yet failed to produce swallowing till it touched the palate—which was spotless. Conversely, the most sensitive tongues I tested were some of *Pyromelana*—which are spotless. (4) My general experience of parent-birds has been that they push the food well into the mouth, and do not merely lay it on the lower mandible, where the base of the twin-spot tongue often lies, pushed forward, when the nestling is asking for food. But I have to make a larger number of special observations before I can suggest that this is invariably the case. (5) The nestlings used were of all ages, from an individual that I took alive from the egg to practically full-fledged birds, and I also used in each case the bills of adult birds of the species. The points of these practically filled the mouths of very young nestlings and gave a simultaneous stimulus at several points. When the nestlings were older, the bill still commonly touched both palate and tongue, and led to swallowing even when inserted beside the tongue, the nestling merely turning its head slightly in that direction. And the bill-point is smaller than numerous objects of food that I have watched the parent-birds push into the mouths of their young.

Altogether, with the best will in the world, I was quite unable to discover any possible use for the spots in relation to the parent-bird, though observation may yet, I suppose, reveal one.

With the flange- and palatal-markings of the Estrildinæ it is quite likely different. The spotted tongues and palates

do not seem specially sensitive, and one has sometimes to push the food well down into the throat to get it swallowed, but the markings are probably in part directive nevertheless. The nests are sometimes distinctly dark, and placing one's eye to the opening one often sees only the brilliantly white stars at the corners of the closed mouths. That these are useful to the parents is likely enough from the fact that the young nestlings especially do not necessarily open their mouths on the nests being touched, but do so at once in reaction to a sharp little touch to the bill between the white stars; and the mouth when opened is yet more clearly indicated by the white flanges. I have seldom myself been able to make out the inner black markings from this position, but it must be different for the bird that has actually entered the nest. In nestlings that I have held in obscurity equivalent (as I judged) to that of the nest, some of the black markings have formed to the eye, a dotted circle surrounding, and to that extent indicating, the gullet; this may, of course, be their function, though one would have thought the vastly more conspicuous white flanges a quite sufficient indication. In *Spermestes poensis*, figured by Bates on p. 590 of 'The Ibis' for October 1911, the encircling black-dotted line is replaced by a nearly unbroken white circle, which certainly seems as though it must be directive. That this is not the whole explanation, at any rate for *Estrilda*, is suggested by the fact that some of the spots by no means come into the "directive" circle, though they certainly contribute to the distinctive appearance of the mouth, and that the circle must, in any case, be dim, except to an enemy that has opened the nest; and by the extraordinary eye-like form taken by the flange-markings in that genus. The opened mouths look like a series of most vicious little demoniac faces, not bird-like at all, with glaring eyes and rows of white teeth. An intimidating element is quite likely present, but "hissing" does not correctly describe the extraordinary, rapid, and continuous click-clacking of the young birds. A final point of great possible interest is the fact that the tongue is

sometimes held upraised so as to show its under-surface and the portion of the lower mandible that in other birds is concealed by the tongue. This gives scope for markings under the tongue, and that these in some cases exist is shown by Mr. Bates's remarks on *Spermestes poensis*. It is probably quite a nice instance of the exception that proves the rule, for in birds' mouths generally, with the under-surface of the tongue concealed, there is a lack there, not only of spots, but of pigmentation generally, just as there is on the extreme under-surface of the whole nestling of *Centropus burchelli*, and on the little-shown under-surfaces of many reptiles, small mammals, and arthropods, and this through no consideration of counter-shading. The confinement of mimicry to seen surfaces (*e. g.* in *Dismorphia*) is exactly similar, and from the facts generally it can be fairly argued that not only the spots, but the pigmentation generally, of the mouths of birds must be for visual effect. It can be argued from the same facts that whether we regard the variations on which the coloration of mouths is originally based as mutations or fluctuations, they can hardly have been large. Strong pigmentation and spots would be harmless under the tongue even if useless, and were these to arise at all frequently by large and sudden variation, we might expect to see them fairly frequently in that position, just as the pigmentation of *Dismorphia* might have been expected not to stop short exactly at the unseen surface if the resemblance had arisen at a leap. Incidentally, the above and other facts connected with the coloration of birds' mouths (*e. g.*, the similarity between the breeding and non-breeding mouths of male *Pyromelana*, in spite of the extraordinary difference in plumage) warn us, at any rate, not to place too implicit a trust in explanations based on correlation. It is also worth while adding that the changes in the mouths are very slow and gradual.

SOME LATER CRITICISMS ANSWERED.

I have lately received the following criticism:—"Among insects a close inter-resemblance between individuals is overwhelmingly the rule, whereas in birds' eggs, where

markings do occur, they are most notably unstable, not only in the same species but in the same nest."

That the objection sounds more formidable than it really is, we may realize at once by remembering how readily, cases of close resemblance apart, we ourselves differentiate by their appearance, most eggs that we know in a given locality. A local collection in which the eggs of each species were so numerous as not to give undeserved prominence to relatively infrequent variations, some of these inseparable from a mode of pigment-deposition that is sensitive to fright, ill-health, &c., would show the same. A very great deal of variability would remain, but certain considerations must be borne in mind:—

(1) Insects are recognized by a definite pattern, eggs by an indefinite one, by the *general effect*. The principle is more suitable for a rollable object which has to convey sufficiently the same visual impression, whichever side is uppermost, and it is probably correlated also with the mode of deposition of the pigment. This very indefiniteness, while it detracts (necessarily) in no way from ease of recognition, gives a far greater latitude to unimportant variation (even as between two sides of the same egg) and quite likely, by the attitude of mind engendered in an enemy, also paves the way for the survival in certain cases, without too great loss, of variation that is somewhat greater.

(2) The very fact that variation often occurs within the clutch will be of advantage to a variable species, by acquainting an enemy with the specific range of variation at a minimum of loss.

(3) A number of insects also, and some insect-groups, are very highly variable, though the variability is often easily explicable on selectionist lines. Even if eggs are much more commonly variable, this merely means more cases to be explained. It is very possible that the explanations will in no way conflict with the theory. It is even possible that important factors may operate in relation to eggs which are not present in the case of insects at all.

(4) Great as may be the variability of eggs, it is never-

theless well to be clear about it. I find that of the Passerine eggs with markings that I am best acquainted with at Chirinda, about 15 per cent. show considerable variability, led by *Pycnonotus layardi*, while 26 per cent. are polymorphic in a more definite way, each possessing two or more forms that are in themselves very constant and between which intermediates rarely occur. The remaining 59 per cent. are really very uniform, apart from rare variations. It must be remembered, too, that even in highly variable eggs there is, in many cases, a common form; also that monochrome eggs are very numerous and seldom very variable. The percentage of variable species will doubtless be higher in some localities and lower in others.

The criticism is a very important one, nevertheless, and I will deal further with variability below.

One might easily go on criticizing. Thus, it might be suggested that it is only in species that do not sit till the clutch is laid, and then only during the first few days, that the matter of egg-coloration will be of importance in relation to enemies; after that it is the parents' coloration that will count. But some parents leave their eggs readily on the approach of an enemy, while others are easily driven off from their nests, and the distinctive element in egg-coloration is, in many cases, only regarded as a last line of defence. The objection is as though one should say that the brilliant displays of many insects when finally at bay are not mnemonic, because at all other times the bright surfaces are concealed by dull-coloured tegmina, &c. It might also be suggested, as a criticism, that egg-eaters will sometimes obtain too few eggs to eliminate the indiscriminate craving already referred to. The objection is again a limited one. Or again, that I probably so surfeited my animals with fowls' eggs that what appeared to be preferences were based only on degree of resemblance, in smell or taste, to the eggs of *Gallus domesticus*. Plausible for the mongoose, the criticism is inapplicable to the rat and lemur, and in any case, it admits a basis of preference. Still, the

lemur's preferences are relatively unimportant, and the rat's might be explained (with a little inconsistency) as having been, very naturally, for those eggs that he was most accustomed to receive. And so on. And yet it is interesting, and in harmony with the theory, that eggs which possess for their first line of defence relative inaccessibility, and particularly *Sitagra's* with the long-necked nest, should have been placed quite high by both animals, while amongst the eggs least liked by each, were some that are very accessible in nature, as those of *Macronyx* (and often *Pycnonotus*, &c.) to the rat, and *Pycnonotus* to the lemur. What is really required, of course, whether for or against the theory, is careful and critical field-observation on the lines of the excellent work of some of our well-known bird-watchers of to-day.

Variability.—Variation in eggs is sometimes local. Thus *Sitagra ocularia* lays only grey-spotted eggs at Chirinda, but red-spotted eggs in some other South African localities. West African Weavers lay some form of eggs that do not seem to figure amongst the eggs of their South African representatives (not that this is necessarily purely a geographical matter), and I was interested lately to see that the forms of *Prinia mystacea's* egg that are rarest at Chirinda are apparently common in British East Africa. Instances could be added from the Catalogue of Eggs.

Variation in the same locality is mainly of two kinds:—(1) definite, as already described for the eggs of many Warblers and Weavers; (2) indefinite. Selectionist explanation would also be of two kinds. Variability may have been selected because useful and necessary; or (2) it may merely have been tolerated as harmless, through a slackening of the factors that make for uniformity.

Definite selection factors making for variability might be the need for the baffling of Cuckoos (possibly an important and somewhat widespread factor), the need for differentiation by parents of their own eggs from those of their neighbours, and procryptic adaptation in varying directions. The existence of the second necessity is doubtful in the case

of the Weavers, and the apparent view of observers that gregariously-breeding sea-birds also recognize their nests by position, with the indirect evidence perhaps supplied by the fact that eggs of the Common Guillemot of the same coloration would seem to have been found in exactly the same spot in successive years, tells against it even here. Extensive experimental transposition of eggs will quickly settle the question.

The question, of course, presents itself: Are these necessities, then, of greater importance than that of ready recognition by enemies? Probably, where nauseousness exists, they are not, but in any case it is rare, I think, to find that where two necessities conflict one merely prevails over the other. Both have to be adequately dealt with, and usually counteragents are found to be present, by means of which one necessity is reduced or both fully met. In the cases under discussion both these methods seem to be in operation. Thus the absence of nauseousness, the fighting qualities of the Drongo and certain other conditions probably act as "reducing" counteragents in the way I shall suggest below, while in some of the Weavers the "enemy" demands are themselves, I believe, boldly met by mimicry, engrafted on to a polymorphism that may have been primarily selected in relation to the baffling of Cuckoos. Again, even if it originated in a common ancestry, the fact that the polymorphic eggs of different species of Weavers and (at any rate at Chirinda) of different genera of Warblers, tend to run to similar forms in the same locality, ensures an ample population and an ample resulting notoriety for each form in relation to enemies, while each *species* still enjoys the full advantage given it by polymorphism in relation to Cuckoos and (if that be a necessity) to parental recognition. At the very worst (if the Cuckoo does try to match her egg—which at present seems unlikely—and is the better enabled to do so through the larger population of each form) the risk is divided up between two or more species. I may mention, finally, the constancy (in my own limited experience) of the non-mimetic forms of polymorphic eggs, amounting in some

cases to that special constancy which one would rather expect to be necessary as a counteragent to the results of any serious diminution of the colour-population. The explanation offered is not incompatible with the view that the phenomenon may be Mendelian. Rather, it perhaps enables us to picture how the necessary basis in heredity for the production of Mendelian results might sometimes have been brought about indirectly by selection elimination.

As for slackness of selection in relation to recognition characters, several things might bring about such a condition. An egg that through the present-day specialization of its enemies or its own loss of nauseousness had become completely acceptable to the former could gain no further advantage from recognition and might vary unchecked. The explanation should be particularly applicable to eggs, for these do not possess those other defences, often slight, yet deterrent to attack by weaker or more replete enemies, of known agility, wings troublesome to remove, chitin a trouble to break up completely, and so on, that are commonly present in the highest-grade insects (except, especially, various geometrid larvæ, themselves often highly variable) and that, as I have actually seen, render easy recognition still useful to them.

Again, there is the case (already suggested) of the bird that has taken to nesting year after year in the same spot in great open colonies. Its enemies would no longer consist of chance passers-by and searchers. On the contrary, the existence of the colony would have become a matter of notoriety and attraction to every enemy in the neighbourhood and far around. Such an enemy would visit the nesting-places whenever it felt hungry enough for a feed of the eggs, the qualities of which it would know well. It would recognise them, not by their coloration, but by their mere presence in the colony, and variation in coloration might once more ensue unchecked. Even if another species with eggs of a different grade should lay in the same colony, the difference in size or shape or texture or general type of

coloration would probably be a sufficient differentiating character.

Merely at first sight it seems corroborative of this explanation that the British sea-birds that form the greatest nesting-colonies—the Common Guillemot, the Kittiwake, and the Black-headed, the Lesser Black-backed, and the Herring Gulls—lay very variable eggs, while the apparently less highly gregarious (or less abundant) Black Guillemot and Common Gull, and the still less gregariously-breeding Great Black-backed Gull, lay eggs that are in the first two cases comparatively, in the third rather markedly, uniform. But there are, of course, numerous other species even of the genus *Larus* to be considered—some laying variable, some uniform eggs, to say nothing of a Tern, *Geochelidon anglica*, that lays variable eggs in South America, but relatively uniform eggs in the north (Cat. Eggs B. M. i. p. 177). Naturally there will often, if not always, be other and complicating factors to be taken into account. That some other species that lay in colonies, as Penguins and Petrels, should lay eggs nearly or quite devoid of pigmentation, is, however, no objection to the view, for loss of pigment might be regarded as an alternative or eventual development when its presence no longer subserves the purpose either of recognition or of concealment*.

Once again, an egg that had become relatively inaccessible to enemies, whether as a simple matter of nesting-site or through the development of pugnacity or fighting-weight in its parents, might similarly not have the same need as formerly for a highly distinctive appearance. In a case of this kind loss of pigment might again be an alternative or eventual development, for there would also be less to fear

* This view may be applicable to many more white eggs than those here mentioned. It has seemed to me, as to Mr. Pycraft, that definite selection must have been at work to produce quite the appearance of, *e. g.*, the eggs of Woodpeckers, the strong distinctive element that appears to me to be present in such eggs pointing to that conclusion; but, obviously, only definite experiment can show whether either of us is correct in his view.

from detection. The Hawks lay very variable eggs; some few of them regularly lay white eggs, and white is not an unusual variation even amongst those species that do not. Still, we have here yet another possible counteragent to variability, a limited one, in the general family resemblance that runs through the many variations. One finds the same thing in the *Acræiinae*, a subfamily of variable butterflies, and hence it was undoubtedly sometimes of use in preventing attack by the birds on which I have experimented. The Fieldfare, a very "fightable" bird (*Wallis*), and one that tends also to nest in colonies, lays rather specially variable eggs, and so do those notorious warriors the Drongos, though here, again, an alternative or supplementary explanation is possible: for in some Drongos, perhaps in all, the variability is of the more definite kind that I am disposed to attribute rather specially to active selection and may perhaps have been in part selected in relation to Cuckoos*.

Finally, there is the probable factor of abundance in a species. It is obvious, I think, that an enemy may become acquainted and remain acquainted with a considerable range of variation in a highly abundant species with, actually and proportionately, a far smaller loss to the latter than would fall to the lot of a scarce species, and that, other things being equal, the selection will be less severe, and the consequent permission to vary greater, for an abundant species than for a scarce one. Certainly most of the more highly-variable species I am acquainted with are also common.

* An objection to this explanation for polymorphism would be that many species in the eggs of which it occurs do not need it for protection from Cuckoos, seeing that none of their eggs are matched by that of any local Cuckoo. It must be remembered, however, that the explanation is only regarded as one of several; that in some cases, too, the form resembled by a Cuckoo may have died out; that other cases may represent a Cuckoo defeated and forced to follow other channels, especially if Cuckoos' eggs should possess the relatively ready adaptability that would seem to be possessed by members of mimetic genera in butterflies, and that, in any case, even a quite distant resemblance should be taken into account, seeing that I found in my experiments that such a resemblance usually sufficed to secure adoption.

At the same time, neither this rule nor any other that I have suggested can be expected to be universal, for other considerations very often are by no means equal. A species that has relatively recently begun to encounter either a more rigid selection or a slackening of selection, is unlikely to show the effects of the change so strongly as a species that has been subjected to these conditions even in a somewhat slighter degree for a far longer period. But degree should be important too. Selection, again, immense as must be its importance as the regulative factor in evolution, is by no means the only thing to be considered. Environment may frequently impose a variability on a species that the latter will only be able to counteract, if at all, by the adoption or accentuation of some defence perhaps quite other than anything suggested above. In such a case as the Fieldfare's (always supposing it to be valid) the additional "fightability" may have been the result of the imposed variability, not this of the other: though in few cases of this kind is it really possible to say which is the cause and which effect, or to do other than suppose that both developed together, reacting on each other.

Great caution is obviously necessary in the interpretation of particular cases. Thus my quotation (above) from Mr. Wallis, which gives Fieldfare, Missel-Thrush, Blackbird, and Song-Thrush as the order of "fightability" for these four birds, is just spoilt as a suggestion of the effect of graded fightability by the fact that the order of variability transposes Missel-Thrush and Blackbird. Either, therefore, relative fightability has nothing to do with relative variability in the four species mentioned, or complicating factors must also be taken into account—as no doubt they must in any and every case. Again, one would have been tempted to suggest the House-Sparrow's egg as an instance of variability resulting from relative inaccessibility, owing to the bird's attachment to human dwellings, were it not for the knowledge that wilderness-inhabiting members of the genus (as *P. arcuatus*) also lay very variable eggs. Every case will

have to be explained with a very full knowledge of the egg's defences, and of the habits of its parents and its enemies ; but I have said enough, I think, to suggest that, if and when the evidence for the existence of preferences in the enemies of eggs becomes conclusive, so far from finding variability a stumbling-block we shall begin to find it reasonably explained.

THE EXPERIMENTS.

Method of Deduction.—If species A was eaten immediately after B's refusal, A was regarded as probably preferred to B. If, however, another acceptance, C, had intervened between B's refusal and A's acceptance, A could not be regarded as necessarily preferred to B. Its acceptance might have been (and often certainly was) the result of a special stimulation of the digestive secretions by C—a stimulation which might even lead to B's acceptance now if reoffered. Depression of the appetite by an unwelcome offering also occurred, and its possibility has to be allowed for, but it was less frequent and less marked than stimulation. Insufficiency of a particular class of prey in the animal's diet before and during the period of experimentation had also to be noted, as it sometimes led to special craving.

Special complicating factors to be allowed for were these : The lemur was found probably to possess a slight preference for freshly-opened eggs as against eggs of the same species that had stood over, opened from the last experiment—not that these were greatly used. The rat appeared to be quite indifferent to this, but slightly preferred fresh eggs to hard-set ones. To this the lemur seemed indifferent. The mongoose, on the other hand, preferred incubated to fresh, and ate readily (as I ascertained by special experiment) even somewhat highly addled eggs of the species he preferred.

I was unfortunate in one of the conditions under which my experiments on the lemur had to be carried out ; fowls' eggs were scarce at the time, and it was, therefore, more

difficult for me to make eggs a really strong item in the animal's daily food, and so avoid that over-eagerness for them that I have referred to, and that was just possibly responsible for the fact that the lemur's preferences were not, as a rule, shown till somewhat near repletion-point. In my experiments on the mongoose this difficulty was not present, and, whether as a result of this or not, his preferences were very marked and decided. So, as a rule, were those of the rat, an animal which from its smaller size was far more easily supplied with an adequate diet than the lemur. I ought to say that I found later that the lemur preferred several species of Noctuid moths and of birds to any of the insects and fruits used in the following experiments, so that it is barely possible that he was sometimes less replete in these experiments than he appeared.

EXPERIMENTS ON A RAT (*Mus rattus*).

Expt. 1. Feb. 2, 1913.—The rat has been a week in captivity and is accepting freely from the forceps. Of eggs he has been offered and has accepted and eaten readily from the very first those of *Amblyospiza albifrons*, *Hyphantornis jamesoni*, and *Coliuspasser ardens*: probably in sufficient numbers to ensure the absence of any undue craving.

Late this morning, having purposely kept him without food since last night, I fed him a very little to avoid acceptances being the result of sheer starvation. He then readily ate a fresh egg each of *Amblyospiza albifrons* and *Coliuspasser ardens*, tasted well and rejected a rather hard-set egg of *Pycnonotus layardi*, and continued to ignore it on my leaving it in the cage, but readily ate a fresh *A. albifrons* egg, repeatedly refused the *Pycnonotus* egg, and smelt and rejected a second of the same species from another clutch, and on my leaving them beside him continued persistently to ignore them. I had to leave, but before doing so added an egg each of *Coliuspasser ardens* and *Amblyospiza albifrons* (each quite as hard-set as the first Bulbul's egg); a Bulbul's egg was left right under the rat's nose.

On my return twenty minutes later the two Ploceid

eggs had been eaten clean out, but the Bulbul's remained untouched and continued so. After waiting a few minutes in vain for further developments, I added a fresh egg of *Colius striatus minor* and withdrew to a distance. I saw the rat turn round and try it, apparently lapping, but quickly turn away again. I went away for five minutes and on my return found the rat's head still averted from the egg and the latter still full. I noticed that a *Hyphantornis* egg (spotted blue type) that I was about to add was probably slightly addled. I put it in with the rest, nevertheless, to see how it would be treated, and beside it a perfectly fresh egg of the same species and form, also a *Coliuspasser* egg, and again withdrew.

On returning five to ten minutes later I found the addled *Hyphantornis* egg and the *Coly* egg overturned and their contents spilling out over the ground, but the other two eggs had been cleanly licked out. I again waited three or four minutes, and as the rat continued to take no notice of the rejected eggs, I added an egg each of *H. jamesoni* (spotted blue type) and of *Crateropus kirki*, first giving the rat a very small scrap of bread, which he accepted from the forceps and ate with greater eagerness than he had shown for any egg.

Twenty minutes later, finding the two eggs still untouched, I tried to ascertain how far he was from actual repletion-point. He ate three or four small scraps of cold maize-porridge, a fair-sized scrap of bread, a little papaw, and some banana—all readily, especially perhaps the last, and the first least, then refused all.

Preferences shown: (1) Partly incubated eggs of *Amblyospiza albifrons* and *Coliuspasser ardens*, fresh eggs of the same two species, and a fresh egg of *Hyphantornis jamesoni* (spotted blue form). (2) Partly incubated eggs of *Pycnonotus layardi* and freshly laid *Colius striatus minor* (only fresh *C. ardens* and fresh *H. jamesoni* were tested against the latter, however).

The above rejections and acceptances, and, finally, rejections of spotted blue *Hyphantornis* and *Crateropus kirki*, took

place when the rat was still somewhat far from repletion. The early rejections were very decided.

Expt. 2. Feb. 3.—Morning. Ate a very small scrap of papaw, tasted and rejected and thereafter refused an egg of *P. layardi*, but readily ate that of *A. albifrons*; refused, then ignored most persistently the Bulbul's egg, but readily ate the blue egg of *Crateropus kirki* (I removed it when half finished), and once more ignored for quite five minutes the Bulbul's egg. I added an egg of *H. jamesoni* (spotted blue form) and left.

I returned twenty to twenty-five minutes later to find the Weaver's egg eaten and the Bulbul's still intact, though left under the rat's nose. I had not time to continue the experiment, but left the Bulbul's egg, and on returning considerably later found it two-thirds eaten. Forty minutes later still, judging him to be distinctly hungry, I gave him a very small scrap (barely more than an eighth of an inch each way) of bread and another of papaw, then placed a Canary's egg (*S. icterus*) in the cage. He neglected this at the moment, and apparently ate none of it during an absence on my part of a few minutes. I therefore added a not dissimilarly marked egg of *Cisticola semitorques*. He at once ate this, then picked up the Canary's egg and ate it too. I put in a second Canary egg and this was ignored, as was a Bulbul's (*P. layardi*), which I added a few minutes later. On my adding a little later a *Crateropus* egg, he turned round as though tempted to try it, actually licked it, and turned away again. On my adding a blue *H. jamesoni* egg, he lapped a very little, and turned away and persistently ignored all four eggs, though I waited away for ten or fifteen minutes. I pushed them up to him in turn on my return, held them to his mouth, and generally tried to coax him to eat them; but he seemed in an irritated condition, bit savagely at the forceps and my fingers, and would have nothing to do either with these eggs or with that of *Sitagra ocellaris*.

An hour later all remained untouched and the rat in the

same corner. I added eggs of *A. albifrons*, *C. ardens*, *Cisticola semitorques* and *natalensis*, *Macronyx croceus*, *Prinia mystacea*, and *Estrilda astrild*, at the same time removing the *Crateropus* egg and those of *P. layardi* and the Canary, and replacing the blue *Hyphantornis* egg by one of the spotted blue form.

In the early afternoon all still remained uneaten, though the rat ate a scrap of bread with the greatest eagerness.

Preferences shown: (1) *A. albifrons*, *C. kirki*, and *Hyphantornis jamesoni* (spotted blue). (2) *P. layardi*. *C. semitorques* was also probably preferred to both *P. layardi* and *S. icterus*; and, after changing his mind and eating the latter, the rat showed signs of great irritation and refused all eggs, though probably far from repletion. Once more the early rejections were of a very decided character.

Expt. 3. Later experiment (8 P.M.).—Found all eggs eaten, except the hard-set *Macronyx*. The shell of this was much broken, but little or none of the contents seemed missing. I added the Canary's egg. This was persistently ignored. I added the remains of the Bulbul's, now, however, commencing to dry. This was eaten, but the Canary's was still persistently refused. The rat readily ate the remains of the *Crateropus* egg (also drying slightly, but less than the Bulbul's), repeatedly and persistently refused the Canary's, readily ate an egg of *Estrilda astrild*, repeatedly and persistently refused the Canary's, ate readily the blue *Hyphantornis* egg, repeatedly and persistently refused the Canary's, ate readily one each of *P. mystacea* and of *Cisticola sub-ruficapilla* (finely speckled), refused persistently a second Canary's egg of the same clutch (the first had just been given to the lemur), ate readily a *C. semitorques* egg (blotched); tasted the second Canary egg on my bringing it again to his notice and rejected it, but readily ate an egg of *Cisticola natalensis* (finely speckled); refused with much apparent annoyance, biting my fingers and the forceps, the Canary egg, but this time also refused one of *Prinia mystacea*, two in turn of *Coliuspasser ardens*, and one each of *A. albi-*

frons, *H. jamesoni* (spotted blue form), *S. ocellaria*, *Cisticola* of the above three species, and *Estrilda astrild*, but ate a bit of porridge. The *Macronyx* egg, lying near him, was ignored to the end. I placed a small feed of porridge in the cage.

Preferences (the Bulbul and *Crateropus* results were quite possibly unreliable, as the eggs were drying): (1) *H. jamesoni* (plain blue and spotted blue), *Sitagra ocellaria*, *A. albifrons*, *Coliuspasser ardens*, *E. astrild*, *Cisticola natalensis*, *C. semitorques*, *C. subruficapilla*, and *Prinia mystacea*—five Ploceids and four Warblers. (2) *Macronyx croceus* (hard-set) and *Serinus icterus*.

Expt. 4. Feb. 4.—This morning I found the bread and porridge eaten, the *Macronyx* egg still uneaten. I removed it, and at about 10 A.M., having just taken another clutch of *M. croceus* (slightly set), experimented again. I first gave the rat two small scraps of bread, then a Canary's egg (*S. icterus*). He refused this most persistently, but accepted and ate a hard-set Bulbul's; he once more smelt and persistently refused the Canary's egg, which had been left in, and this time refused as persistently a fresh Bulbul's egg and a *Macronyx* egg from the new clutch; refused a *Crateropus* egg, but readily ate a spotted blue egg of *H. jamesoni*, and once more refused persistently the *Macronyx* and *Crateropus* eggs. I could not re-offer the Bulbul's egg, as the rat had passed over it and broken it. He made no attempt to lick up the contents. I now put in an egg of *H. jamesoni* (spotted blue). He ignored this for some minutes, and I went to lunch. I returned in the middle of the meal—perhaps a quarter of an hour—and, finding it still uneaten, added that of an *A. albifrons*. Returning probably twenty minutes later I found this egg completely licked out and the other either half-eaten or half-split—it was overturned. I added a *C. semitorques* egg (white with large blotches) and another *A. albifrons*. There was considerable delay before either was touched. Finally, I found the *A. albifrons* egg nearly completely eaten and the rat now ignoring both. I removed them.

Apparent preference :

	1. <i>Amblyospiza albifrons</i> .	
	2. <i>Hyphantornis jamesoni</i> (spotted blue).	} <i>Cisticola semitorques</i> .
} <i>Crateropus kirki</i> , <i>Macronyx</i> (fresh).	3. <i>Pycnonotus layardi</i> (hard-set).	
	4. <i>Macronyx croceus</i> (hard-set) and <i>Serinus icterus</i> .	

Expt. 5. Feb. 4. Later experiment, 8 P.M.—No food since last experiment. Most persistently and for a very long time refused the Canary egg, very readily ate one of *C. ardens*, continued to ignore that of the Canary, gnawed slightly and rejected a leg each of small nestlings of *A. albifrons* and *Colius minor*.

Preferences :

1. Egg of *Coliuspasser ardens*.
2. „ *Serinus icterus*.

Nestlings of *A. albifrons* and *Colius minor* were rejected when the rat must have been still far from repletion-point.

Expt. 6. Feb. 5.—Gave only a small feed last night to rat (of water-made maize-porridge only, no animal food) and nothing this morning. At 8.30 A.M. I began to experiment. I first inserted the cream-coloured egg of *Chalcopelia afra*, nearly fresh, and the rat ate a third of it, lapping and stopping, lapping and stopping, before I removed it. I allowed three or four minutes for possible after-effects, and re-offered the egg. Another third was now eaten before I again removed it, and offered a diminutive scrap of bread, which was at once hungrily accepted and eaten. On my replacing the Dove's egg in the cage, the rat again began to eat it and I again removed it. I offered the Canary egg. I had only one left intact, and what remained of yesterday's was drying up. I accordingly blew a greater part of the former (fairly hard-set) into the latter's shell and offered this. The rat at once ate out all its contents—those of the other egg and its own,—ate two small scraps of bread, ate without hesitation the remaining contents of the new Canary egg; commenced to eat also a slightly hard-set egg of

M. croceus (yesterday's clutch), but I withdrew it; ate a *C. semitorques* egg (blotched) left uneaten from yesterday and the remains of the *Hyphantornis* and *A. albifrons* eggs of yesterday (a good deal less than half in each); ate the whole of the remainder of the *Macronyx* egg and the rest of the Dove's, then another *A. albifrons* and neglected the next, as also one of *H. jamesoni* (spotted blue) and one of *C. ardens*. Later he had eaten part of the latter and was now neglecting it, and he also neglected an egg of *C. ardens*. He similarly neglected, as persistently, the eggs of *P. mystacea*, *Cisticola semitorques* (practically spotless, pale blue, unusual), *C. afra*, and *M. croceus*. He became irritable at the end, and knocked the last two eggs right away with his fore feet, and kept gnawing savagely at the ground. Whether these symptoms of irritation were provoked by my insistence, by dislike of the eggs offered, or by internal happenings, I was unable to judge. He also refused to touch bread, either in scraps or in large pieces, even when placed in his cage.

The sun now began to break through the clouds, and as it had been very cold in the verandah I put him out. He soon began to show much liveliness, and attacked and finished the bread—two or three of the pieces being fairly large.

This lapse into apparent indiscriminateness was puzzling. I have seen the same thing happen in the case of a Butcher-bird (*Lanius collaris*), normally discriminating, in relation to highly nauseous insects. It may conceivably have been due to a lack of the animal element in the rat's diet during the last twenty-four hours (except for last night's *C. ardens* egg), or, very likely, it may not.

Expt. 7. Feb. 5.—I left in a hard-set *Macronyx* egg from the first clutch. The rat ignored it for a long time. I added an egg of *A. albifrons* and went away. On my return fifteen minutes later both eggs remained untouched. I added an egg of *S. ocellaria* (typical coloration), and, being still busy, left for twenty minutes. On my return I found the last-named egg licked clean out, and the other two still

being ignored. The rat continued to ignore them, and I finally removed them.

Apparent preference :

1. *Sitagra ocellaria*.

2. *Amblyospiza albifrons* and *Macronyx croceus*.

Expt. 8. Evening, 8 P.M.—No food since the afternoon experiment ; accepted and readily ate a fresh egg of *A. albifrons*, refused the hard-set egg of *M. croceus*, and continued to ignore it persistently for perhaps fifteen minutes, but at once accepted and ate an egg of *A. albifrons* which I now added to that of the *Macronyx*. I next added to it two *C. ardens* eggs—one fresh, the other hard-set, and each (as always) opened.

The rat selected the hard-set Whydah egg and ate it, and I added an egg each of *Prinia mystacea*, *C. semitorques* (unspotted), and (again hard-set) of *C. ardens*. The rat selected the *Prinia* and ate it. I now had to discontinue the experiment and removed the eggs.

Apparent preference : (1) *Amblyospiza albifrons*, *C. ardens*, and *Prinia mystacea*. (2) *Macronyx croceus*. The experiment was not continued long enough to ascertain whether *C. ardens* and *C. semitorques* were really less liked than the *Prinia*. It may have been merely a selection of one of three species, for all of which he was sufficiently hungry.

Expt. 9. Feb. 6.—I gave the rat last night, in addition to his porridge, as animal food, a good many small grasshoppers of the species best liked by my birds. No milk. He had eaten all the grasshoppers when I looked this morning.

I was busy close by throughout this experiment, and simply ran every three or four minutes to see what was happening.

The rat at once accepted a nearly fresh *Sitagra ocellaria* egg, and refused yesterday's hard-set egg of *Macronyx croceus*. I returned later two or three times, and still always finding it uneaten added one of *Amblyospiza albifrons*. This was at once eaten. I now left in the *Macronyx* egg alone, and returning later found that its solid contents

had been pulled out and were lying, damaged but now neglected, beside it, while the rat had returned to the empty shell of the *Amblyospiza* egg, and was assiduously licking out its inside. Returning three or four times I every time found the *Macronyx* egg and its extracted contents lying untouched, the rat close to it but completely ignoring it. I therefore added a second, only slightly set *Macronyx* egg from the second clutch, opening it slightly as usual. This was as persistently ignored as the other, so I added an egg, just slightly set, of *Chalcopelia afra* (from the same clutch as yesterday). This was also persistently ignored (it may, of course, have been *tasted* in my absence), and after two or three visits I removed the fresher *Macronyx* egg and pushed the other slightly away, leaving the Dove's egg alone just under the rat's nose. He still refused it, so two or three visits later I placed beside it an egg of *A. albifrons*, very slightly set. This was at once taken and eaten. I placed the fresher *Macronyx* egg beside the Dove's, and both were now persistently ignored. I replaced the *Macronyx* egg by one of *H. jamesoni* (spotted blue) and the latter's contents were at once completely eaten. I again inserted the fresher *Macronyx* egg, and it and the Dove's continued to be neglected. I placed beside them a fresh *C. ardens* egg and went away for twenty minutes. Returning I found only the Whydah Bird's eaten. The hard-set *Macronyx* egg and its embryo had been lying conspicuously a little to one side throughout the experiment, and remained untouched not only up to this point but about twenty minutes later still, when I removed it.

Later.—To-night I am again giving the rat water-made maize-porridge *only*—no animal food. The idea is to see whether it will affect his discrimination to-morrow.

Preferences shown (very decidedly) :

1. *Amblyospiza albifrons*, *Hyphantornis jamesoni* (spotted blue), and *Coliuspasser ardens*.
2. *Macronyx croceus* (both hard-set and nearly fresh), *Chalcopelia afra* (nearly fresh).

Expt. 10. Feb. 7, 10 A.M.—No food since last night's

porridge. I was busy again, and after the first few acceptances was only able to return at considerable intervals.

The rat, ravenous in manner, at once ate an egg of *Sitagra ocellaria*; licked out a portion of a slightly hard-set Turtle-Dove's egg (*Turtur damarensis*) that, for convenience of insertion in the cage, I had blown into an *Amblyospiza* shell painted with black patches of water-colour for the sake of distinctiveness; refused to touch some water (offered to guard against the possible complication of thirst—as his supply of water was finished), and, so long as I remained present, refused yesterday's egg of *M. croceus*; but he at once ate another *Sitagra* egg. I left for some time, and on my return found the *Macronyx* egg eaten and lying to one side, but by no means licked out like the *Sitagra*'s. The rat then licked out another very small portion of the *T. damarensis* egg, and refused persistently to attack an egg of *Chalcopelia afra*. I left for at least twenty minutes, and on my return found it still uneaten; but a further small portion of the *Turtur*, now inserted, was licked out of a shell coloured as usual. I once more left for a very considerable time, and returned this time to find the rat just lying down, after eating the *Chalcopelia* egg. This, too, was by no means cleanly licked out. Another small portion of Turtle-Dove's egg was then licked out, but the rat after this refused all eggs (including *C. ardens*, *S. ocellaria*, and blue *H. jamesoni*), burying his head in a corner whenever I brought one up to him.

This was nearly two hours after the commencement of the experiment, such had been the interruptions. I left in the cage three *Coliuspasser* eggs (one fresh, one hard-set, one medium), the blue *Hyphantornis* (fairly hard-set), and the *Sitagra ocellaria* egg (fresh). Nearly half an hour later (12.25 P.M.) a quarter of the latter had been eaten, and it was now lying abandoned and the rest remained quite uneaten, though the rat showed great eagerness for a small scrap of brown bread, which he ate. At about 2 P.M. all were still uneaten and I added a fresh *Amblyospiza* egg. At 3.30 P.M. only this had been eaten, and the rat continued to refuse the others. He accepted readily and commenced to

nibble a grain of buckwheat—I could not see if he finished it; accepted with disinclination, and began to eat a leg of a nestling *A. albifrons*, and eagerly ate a scrap of bread; afterwards returning to the Weaver leg, but relinquishing it at once in favour of a second scrap of bread. He finally finished the leg and ate more bread.

Comment.—“ I was able to give too little consecutive time to the experiment. Preferences were shown, and the long delays must also be taken into account as conducing to hunger. At the same time the experiment seemed to me to bear some resemblance to that of the day before yesterday. Does the rat have his rash days, or is it merely the result of too little animal food during the preceding twenty-four hours? ”

Apparent preferences: (1) *Sitagra ocularia* and *Turtur damarensis*. (2) *Macronyx croceus*. The *Turtur* appeared to be preferred, too, to *Chalcopelia*, and a preference was shown at the end for fresh *Amblyospiza* as against *Coliuspasser* (new-laid, medium, and incubated), blue *Hyphantornis* (fairly fresh), and *Sitagra* (fresh). •

Expt. 11. Feb. 8.—Gave the rat a large and varied feed at 8 P.M. yesterday evening, both animal and vegetable. The former consisted of a head and leg of a small nestling *A. albifrons*, several grasshoppers of the pleasanter species, and milk—the vegetable food of maize-porridge and banana. An egg of *C. ardens* was also left in. This morning all had been eaten, except a small scrap of banana.

I added, fairly early in the morning, a very hard-set egg of the *Coliuspasser*. This was neglected, and continued to be so for some time. Eventually I noticed it had fallen behind the tray, and not wishing to disturb the rat overmuch, as I intended to experiment, did not attempt to ascertain whether it had been emptied or not. Later in the day I noticed it was eaten.

At about 11 A.M. I broke down the side of yesterday's *T. damarensis* egg to the level of the liquid (it was more than half-full still and less hard-set than I thought yesterday) and inserted it. The rat lapped a few times, then abandoned

it, and shortly afterwards lapped again and abandoned it. No further developments occurring, I went away and, returning considerably later, found the egg pushed aside, but no noticeable further diminution in its contents. I placed beside it an egg of *C. ardens*, somewhat set, which was at once attacked and eaten. I replaced it with a nearly fresh egg of *Dryoscopus guttatus*. This was tried, then neglected. I went away for a short time and on my return found the *Dryoscopus* egg two-thirds eaten. The remainder had been abandoned. I left in beside it a second egg from the same *Dryoscopus* clutch, and this was shortly afterwards tried and at once rejected. As the rat took no further notice of it I went to my work, and simply returned two or three times at intervals, one or two of them as long probably as half an hour. The *Turtur* egg and the two of *Dryoscopus* remained untouched beside the rat throughout, except that I once found the *Turtur* egg somewhat shifted—but with no appreciable diminution in its contents. I then added an egg of *A. albifrons* which was not attacked during the three or four minutes during which I watched it, but had been eaten when I returned half an hour later, though the others remained untouched.

I now left in the Dove's egg alone for a considerable time, and it remained untouched. I put in again first one *Dryoscopus* egg and later the other. The second was lapped at and refused; otherwise both were neglected, though pushed in turn under the rat's nose and left there. I then put in a half egg, very slightly set, of *Centropus nigrorufus*. The egg closely resembled the Dove's both in size and colour, and I therefore mottled it over with red water-colour paint to give it a distinctive appearance. Even so, owing to its being only a half egg longitudinally cut, very little of its outside probably showed, and the general impression was doubtless that of a Turtle-Dove. Whether for this reason or on its merits (I did not actually see it tasted) the egg remained uneaten, though left in for a very considerable time. So did one of *Telephonus senegalus*. That of a Whydah Bird (*C. ardens*), very hard-set, was, however, attacked and had its

more liquid portions eaten, the solidest parts of the embryo being left uneaten on the ground. The rat then ate a nearly fresh egg of *H. jamesoni* (Bulbul-like form) which I added to the others, and a little later had eaten a portion of a fresh egg of *Coliuspasser ardens* with which I replaced it. This was now being neglected, but I put in beside it a fresh egg of *T. senegalus*, and a very little later found the *Coliuspasser* egg finished, but the *Telephonus* egg quite uneaten. Some considerable time afterwards I found a very small portion of the *Telephonus* egg eaten, the rest abandoned. I left all in together for a considerable time, and, as there were no further developments, added the eggs of *S. ocellaria* and *Hyphantornis jamesoni* (Bulbul-like form). These were eventually eaten, the others remaining untouched to about 4 P.M., when I removed all but the Dove. This is still uneaten this evening.

Apparent preferences: (1) *S. ocellaria*, Bulbul-like *H. jamesoni* (nearly fresh), *C. ardens* (fresh and hard-set—the solid portions of the latter egg were neglected), *A. albifrons*. (2) *Turtur damarensis*, *Dryoscopus guttatus*, *Telephonus senegalus*, and probably *Centropus nigrorufus*.

Expt. 12. Feb. 9.—Gave the rat a large mixed feed again last night. A little was left in the morning. At about 9 A.M. I commenced to experiment, placing the practically fresh egg of *Colius minor* in the cage. The rat tried and at once left it, and continued persistently to ignore it. I later added to it a fairly hard-set egg of *P. layardi*. This was equally persistently ignored, probably, from the slightly altered look of the opening, after tasting, and a very Bulbul-like egg of *H. jamesoni* (rather set), that I showed off to the rat before inserting it, was also continuously ignored. I next showed him and inserted a fresh *white* egg of *H. jamesoni*. After a little hesitation the rat tentatively tried it, and then at once pulled it from amongst the other two, and ate the whole of its contents. There was a possibility that the freshness or otherwise of the eggs had influenced the rat's decisions, so I inserted a beautifully fresh egg of *Colius*

minor (there had only been one in the nest). I had no new-laid Bulbul's eggs to offer. This Coly egg was at once tried and rejected, and the rat refused to have anything more to do with it. After an interval, during which no developments took place, I added a medium hard-set egg of *H. jamesoni* (Bulbul-like form). This was also at first ignored, and I added a perfectly *fresh* egg of the same form and a fairly hard-set egg of the white form. The somewhat set Bulbul-like egg was the next to be selected and eaten, in spite of its coloration.

A little later, as there had been no further developments, I removed the remaining (first-inserted) Bulbul-like hard-set egg and the white hard-set egg of *H. jamesoni*, and put in instead a fresh egg of *T. senegalus* from a different clutch from yesterday's. I went away for quite an hour and on my return found that nothing had happened, unless, possibly, the opening of the *Telephonus* egg had been slightly enlarged, indicating trial. I now left in the cage simply the Bulbul egg, the fresh Coly egg, and an egg of *D. guttatus*. Nothing having happened, I added the *Telephonus* egg. Again nothing happened, and I gave the rat a maize-grain, which was eaten. The eggs were again ignored, and I added two fresh eggs of *H. jamesoni*, one spotted blue, the other of the Bulbul-like form, both fresh. The rat at once ate the former, but continued to ignore the second, as also a *Coliuspasser ardens* egg and one each of *S. ocellaria*, *Cisticola semitorques* (a Stonechat-like form), *Prinia mystacea*, and *Estrilda* sp., which I now added at short intervals. Looking in soon after adding the last, I saw that the *Coliuspasser* egg had been eaten—possibly (without my noticing it) before some of the last additions.

As a little time now elapsed without further developments, I removed all the remaining eggs. The rat ate three maize-grains and a small piece of brown bread and butter, but refused to go on with this, and had, in fact, shown some disinclination for the mealies too—as yesterday. He had not been greatly inclined for eggs generally—probably the

result of his feeding in the night,—but to-day again there seemed no reason to doubt the preferences so clearly shown. They were

(1) *Hyphantornis jamesoni* (white form, spotted blue form, and one, rather set, of the Bulbul-like form), and *Colius passer ardens*.

(2) *Pycnonotus layardi* (fairly hard), *Colius minor* (nearly fresh and very fresh), *Telephonus senegalus* (fresh), *Dryoscopus guttatus*. Neglect of Bulbul-like eggs of *H. jamesoni* was perhaps due to their resemblance, closer than the white forms, to a Coly's or Dove's.

Expt. 13. Feb. 9, evening.—Refused persistently a hard-set egg of *P. layardi* and a fresh egg of *C. striatus minor*, but readily ate a fresh *T. senegalus* egg, then refused persistently one egg each of *P. layardi*, *C. striatus minor*, and *D. guttatus*. On my adding another egg of *T. senegalus*, this, too, was persistently ignored. Later I added one of *A. albifrons*, which was treated in the same way, as was one of *H. jamesoni* (Bulbul-like form) added a little later. But a *Sitagra ocellaria* egg added to them was at once eaten.

Apparent preferences :

- | | |
|---|--|
| 1. <i>Sitagra ocellaria</i> . | |
| 2. <i>Telephonus senegalus</i> . | |
| 3. <i>Pycnonotus layardi</i> (hard-set) and
<i>Colius minor</i> (fresh). | } <i>Amblyospiza albifrons</i> ,
Bulbul-like <i>H. jamesoni</i> . |

It would be interesting to know if the acceptance of the first *Telephonus* egg was unregretted and to be relied on.

Expt. 14. Feb. 10.—Morning: after a mixed but not large feed last night (*A. albifrons* nestling's head, six maize-grains, milk, two good-sized grasshoppers). Refused persistently, first a Coly egg alone, then the Coly egg and a Bulbul egg, then a nestling Bulbul two days hatched, then a part of a slightly older but quite unfledged *A. albifrons* nestling, and, finally, an egg of the last-named species and one of *C. ardens*.

CONCLUSIONS FROM EXPERIMENTS ON THE RAT.

The rat's preferences in eggs were more marked than the lemur's, the unwelcome eggs being in some cases allowed to lie neglected for many hours together, even when the animal was more or less hungry; and, again unlike the lemur, the rat did not require to be fed nearly to repletion before he would begin to discriminate. A marked exception to this rule occurred on Feb. 5th, when the animal lapsed into complete indiscriminateness. An insufficiency of animal food during the preceding twenty-four hours, in combination with the bitterly cold day, suggested itself to me as an explanation, and I tested this in my subsequent dieting of the rat, but it may not be the correct one. At any rate, he usually discriminated and was consistent, and it is possible to set forth approximately the preferences shown in the form of the following table—not that the material used in these experiments was sufficient to justify us in supposing that their results necessarily represent what would have been the rat's final verdict on all the species used. Still, the lemur's general confirmation of the rat's preferences seems to show that—at any rate, in the main—they represent the impression the eggs would make on an egg-eating animal, and a second rat, on which, owing to its extreme wildness and the limited supply of eggs, I did not continue to experiment, showed exactly the same initial eagerness for the eggs of Weavers and the same dislike for an egg of *P. layardi* :—

<i>Estrilda astrild.</i>	1. <i>Sitagra ocularia.</i>	} <i>Coliuspasser ardens.</i>	
<i>Cisticola natalensis,</i>			
<i>subruficapilla,</i>	2. <i>Amblyospiza albifrons.</i>	3. <i>Cisticola semi-</i>	
<i>Prinia mystacea.</i>	3. <i>Hyphantornis jamesoni</i>		<i>torques.</i>
<i>Turtur capicola.</i>	4. {	4. <i>Crateropus kirki,</i>	4. {
		<i>Tel. senegalus,</i>	
	5. <i>Pycnonotus layardi,</i>	<i>guttatus,</i>	
	<i>Colius striatus.</i>		<i>Centropus.</i>
	6. <i>Macronyx croceus, Serinus</i>		
	<i>icterus, Chalcopectia afra.</i>		

On one occasion only, I think, *Amblyospiza* was eaten in preference to *Sitagra*.

The Bulbul-like form of *Hyphantornis jamesoni* rather specially tended to be refused—perhaps the result of the likeness, which was usually better than the resemblance borne by, *e. g.*, the white form to the other white eggs of the experiments.

The eggs of all but three species in this list are always or very frequently laid within ordinary climbing range of a rat.

EXPERIMENTS ON AN INDIAN MONGOOSE.

Expt. 15. June 27, late afternoon.—Ate readily a minute scrap of beef, then ate eggs of Grey Wagtail and Blackbird. Smelt and refused Fowl's egg, even a small portion in a spoon, but ate with much smelling and tasting a Hedge-Sparrow's; then smelt and refused all eggs I could offer, including not only the above species but a Great Tit's, a Wren's (*Troglodytes parvulus*), and others. But he ate with some slight eagerness a common mouse, and, with distinctly greater eagerness, a piece of beef.

On the two previous days that he has been in my possession he has on several occasions eaten beef in strong preference to mice, and with eagerness even when the latter had been actually refused.

Order: (1) beef; (2) common mouse; (3) *Accentor modularis*'s egg, probably preferred to (4) that of *Gallus domesticus*. Great Tit's, Wren's, and Grey Wagtail's eggs were also below (2).

Expt. 16. June 28.—I left the mongoose for food last night only a Fowl's egg. It is still uneaten. The animal smelt and refused in turn fresh eggs of Spotted Flycatcher, Wren, and Fowl, but ate readily, after smelling and tasting it, a partly-incubated House-Sparrow's egg; smelt and refused fresh eggs of Spotted Flycatcher, Wren, Fowl, and Grey and Pied Wagtails, but smelt and most readily ate a fresh House-Martin's egg. Smelt and refused all as before, also one each of Willow-Warbler, Hedge-Sparrow, and, less decidedly, Song-Thrush; but, on smelling it, ate with eagerness a fresh House-Sparrow's egg, returning to the empty shell again

and again, and licking it out or crunching it, while still ignoring the various rejected eggs placed before him. Repeated his previous refusals up to and including Hedge-Sparrow, but, with some hesitation, started on the Thrush's and ate it. I removed it before it was quite finished and repeated the offerings. All were refused but the Thrush's, which was accepted and finished, but not licked out exhaustively like the Sparrow's. Following this, the mongoose started on the Hedge-Sparrow's, but did not finish it. He then repeated his various refusals, including Hedge-Sparrow's, but *readily* ate another freshly-laid House-Martin's, returning to it and frequently licking it out, etc., as before, long after it was emptied, and again repeated all his refusals. This time, several of the previously-refused eggs were refused at sight—an important point. I, nevertheless, held them persistently to his mouth till each was definitely smelt and refused. I obtained in this way an actual tasting of the Flycatcher's (followed by a prompt rejection) and a scrunching between the teeth of the Pied Wagtail's, the mongoose then throwing it right down and shaking his head. I had placed each egg on the ground under his nose as it was refused, and he now smelt them all over and refused to touch any but the Hedge-Sparrow's, which he returned to and ate. I then picked each up in turn and offered it, again placing each below his nose as he refused it—and he refused every one. Finally, I offered another House-Martin's egg, and this was at once accepted and eaten. After a yet further repetition of his various refusals, he went on to eat a very hard-set *Sylvia simplex* egg (its advanced state of incubation may, of course, have influenced this acceptance); then once more repeated his refusals, but ate beef with even greater eagerness than he had shown for anything else.

I left in the cage the various species of egg used, excluding Hedge-Sparrow, Thrush, House-Martin, and Sparrow, and, one-and-a-half hours later, found the Flycatcher's broken but not eaten, the two Wagtails' broken and possibly eaten (a moisture on the ground was not necessarily theirs), and only

two eggs left intact, but both overturned—the Wren's and Willow-Warbler's.

I think I can say that during the main experiment the mongoose once or twice showed slightly more inclination to try the Flycatcher's and Wagtail's eggs than the Wren's or Warbler's; one or two actual tastings (followed, it is true, by rejection) were obtained.

Order: (1) beef (to judge by manner); (2) *Chelidon urbica* and *Passer domesticus* (both new-laid); (3) *Turdus musicus*; (4) *Accentor modularis*; (5) *Muscicapa grisola*, *Motacilla sulphurea*, *M. alba yarrelli*, *Troglodytes parrulus*, and *Phylloscopus trochilus*, the last two possibly least liked; also *Gallus domesticus*.

“I was a little surprised,” I wrote, “at the relatively high placing of Thrush and Hedge-Sparrow and the very low placing of Wren and Willow-Warbler. Of course, one does not yet know how many or how few grades may come below the latter, while there are quite probably gaps to be filled between grades 2 and 3. At any rate, I could in no way complain of the experiment, it being, as regards decided and unequivocal action on the animal's part, as good as any I have ever carried out. The contrast between grades 2 and 5 was very strongly marked, and lasted to the end of a longish experiment—for the short account I have given does not convey a full idea of the re-offering and coaxing that took place to give the mongoose every chance of reconsidering his refusals. Two different Wren's eggs were used, three Spotted Flycatcher's (from two clutches), only one Willow-Wren's, but two of each kind of Wagtail, and three Martin's. In every case the mongoose's treatment of eggs of the same species was identical—excepting that he grew hungry enough for the Thrush's and Hedge-Sparrow's, at first refused.”

Expt. 17. June 29.—Last night I left in the cage, as well as meat (duck), a fowl's egg and a duck's egg. The meat and a considerable part of the fowl's egg were eaten by this afternoon, the duck's egg untouched. I had made a large hole in each egg and placed them side by side.

To-day (late afternoon) I offered some fowl's egg (both yolk and white) in a spoon. The mongoose ate a little and desisted, refusing to touch it again, smelt and refused an egg each of Wren, Willow-Wren, Grey Wagtail, and Pied Wagtail, but smelt and proceeded to eat a Spotted Flycatcher's; again refused the two Warblers' and the two Wagtails', but at once commenced to eat another Spotted Flycatcher's; smelt and refused all as before, also the fowl's, but at once, after smelling it, commenced on a Spotted Flycatcher's from another clutch. I removed this, and he repeated all his refusals, but smelt and began to lick out a Hedge-Sparrow's egg that I held out to him. He soon desisted, however, and at this moment I accidentally dropped it between his fore feet. He ignored it, however; then repeated all his previous refusals, but with real eagerness (in marked contrast to his acceptance even of the Flycatcher's eggs) attacked, on smelling it, a House-Martin's egg. He not only licked up its contents with the greatest rapidity and zest, but kept returning to the empty shell and licking and licking it, or crunching it further as a preliminary to yet further licking. I next offered a nearly unspotted Wren's egg. Deceived possibly by the white colour, he came forward with the greatest alacrity, but withdrew promptly on smelling it. He then smelt and refused a Willow-Wren's egg, the Wren's again, and both Wagtails', but accepted and ate a Spotted Flycatcher's. I let him finish it—the Hedge-Sparrow's was still lying ignored, possibly unnoticed (being far back),—and again offered the fowl's egg in the spoon. This time he ate a little of it, but quickly desisted, and, on my pressing it on him, rejected it with a flick of his tongue below the spoon—an action I have seen my cat employ in rejecting birds.

The mongoose then smelt and refused all as before, but smelt very thoroughly and attacked a somewhat incubated, but also somewhat stale, Sandpiper's egg, going on with it with some eagerness once he had started. I removed it very soon, and he then repeated all his refusals, but smelt and readily attacked a somewhat incubated Blackbird's egg;

then, with an appearance of increased appetite, once again attacked the portion of a fowl's egg re-offered in a spoon. He showed (as he has done before) a marked preference for the yolk, and desisted when he had finished such as was present. He neglected most of the white.

The order suggested was: (1) *Chelidon urbica*, easily first. It is quite likely that three or four grades may be found to intervene between this and (2) *Muscicapa grisola*. In these grades, as in (2), would come the half-incubated Blackbird's egg and the half-incubated and somewhat stale Sandpiper's egg (not a fair test) of this experiment. (3) *Accentor modularis* and *Gallus domesticus*. (4) *Motacilla yarelli* and *M. sulphurea*, *Troglodytes parvulus* and *Phylloscopus trochilus*.

With the exception of the Sandpiper's, all the eggs used were fresh, and, with the exception of that egg and the Blackbird's, all were quite unincubated. The placing of the Hedge-Sparrow's was not quite convincing, owing to its unfortunate escape; therefore it cannot be regarded as quite certain that it has now been placed below the Spotted Flycatcher's in the mongoose's estimation, though that is probable.

Expt. 18. June 30.—In the night the mongoose again ate all the meat he was given and a fowl's egg, but again ignored a duck's egg. At 11 A.M. to-day I commenced to experiment. He smelt and refused a Pied Wagtail's egg; smelt and refused the same broken into a spoon, the shell removed, beautifully pellucid and fresh; smelt and refused a Wren's egg and again the broken Wagtail's, going on to refuse it persistently even when pushed right up to his nose; refused a Spotted Flycatcher's at sight, but on my pressing it on him he inserted his tongue and ate much of it readily enough before I removed it. He at once, then, began to eat the broken Wagtail's too, but quickly desisted and refused it persistently, though he at once attacked and finished the Flycatcher's re-offered. He then again tackled the Wagtail's, but quickly stopped, having diminished it to no appreciable extent by these two attacks. It should be

remarked, however, that even the Flycatcher's was not licked out with great thoroughness yesterday or to-day: this may be contrasted with his treatment of House-Martins' and Sparrows' eggs.

He next ate a portion (all I offered) of a Kestrel embryo nearly ready to hatch, ate a very little of the white of the broken Wagtail's egg (in this case he ignored the yolk), then desisted and refused to eat more; smelt and refused Grey Wagtail's and Wren's, and, on my leaving them under his nose, ignored them, then reached right over and past them to a wing of the Kestrel embryo that I had previously dropped, then (stimulated?) bit into but relinquished without eating it the Grey Wagtail's egg and continued to ignore it and the others.

Fifteen minutes later the eggs of the Wren and Wagtail were still being ignored. He smelt and refused the Pied Wagtail's egg in the spoon (definitely offered), licked up a little white of a duck's egg in another spoon, repeated all his usual refusals, also Willow-Wren, but ate a somewhat hard-set Blackbird's egg.

He smelt and refused eggs of Wren, Grey and Pied Wagtail, and Willow-Warbler, but smelt a Spotted Flycatcher's egg, and, on my putting it down on my side of where I had placed the Wren's and Grey Wagtail's, leaned over them to it without rising completely from his bed and tried to lick it out. He could not avoid getting sand on to it, however, so drew back and smelt and refused each of the others, then leaned forward again to the Flycatcher's, and, stretching out a paw, drew it towards him up to and between the other two (separating them with it as he pulled it through), and there licked it completely out, took a lick or two at the Grey Wagtail's but at once desisted; smelt and refused the Wren's egg as it lay there, and again licked out assiduously the already empty Flycatcher egg—presumably hungrier than on previous occasions.

Apparent order of preference: (1) *Muscicapa grisola* (fresh); *Falco tinnunculus* (ready to hatch); *Merula merula* (semi-incubated); Domestic Duck (fresh). (2) *Motacilla*

jarrelli, *Motacilla sulphurea*, *Troglodytes parvulus*, *Phylloscopus trochilus*.

The apparent preference for fowls' eggs against ducks', which the mongoose's nightly choice seems to indicate, may be more apparent than real. It can only be tested by definite experiment.

Expt. 19.—The following experiment was an uninterrupted continuation of that just described, but, as the eggs used were, purposely, mostly stale ones, it will be best to describe it separately.

A possible objection to the reality of such preferences as were being shown had struck me: even though to human senses every egg offered might be equally and perfectly fresh, might not a day or two's difference in their taking be perceptible to the mongoose, and be what really decided him to take some and leave others? I had some more or less addled eggs on hand, so it seemed well to test the point more fully than I had done with the Sandpiper's egg.

The experiment was long, and in many ways highly interesting; but, as stale eggs are "not evidence," I will content myself with summarizing it.

Amongst addled eggs, Garden-Warbler, Hedge-Sparrow, Bullfinch, House-Sparrow, Golden Plover, Common Sandpiper, Oyster-catcher, Pheasant, and Red Grouse were eaten more or less readily, even eagerly; while Great Tit and Eider-Duck (and the new-laid eggs mentioned below) were consistently refused. Amongst practically fresh eggs, House-Sparrow and Bullfinch were thus preferred to Great Tit and Eider. Two highly incubated eggs (Garden-Warbler and Kestrel) were both placed high. Amongst new-laid eggs, Pied Wagtail, Grey Wagtail, Wren, Willow-Wren, and Domestic Duck were all refused throughout a long experiment, and Spotted Flycatcher and Lesser Whitethroat were similarly refused, but were not necessarily placed as low as the others, as the mongoose was now filling up, though he still, after refusing them, ate nearly fresh Sparrow and Bullfinch eggs and addled Hedge-Sparrow and Grouse.

An apparent preference was shown early for the less

added of two Great Tit's eggs, but practically none of it was eaten, so that it can hardly count for much; and the rest of the experiment showed clearly that the mere fact of being stale—even highly so—did not act as a deterrent to this animal.

Expt. 20.—In the early afternoon the mongoose smelt and refused duck meat, a duck's egg, a nearly fresh Eider's, a Wren's, Grey and Pied Wagtails', Willow-Warblers', Great Tits', etc.; all but the Eider's were new-laid. He eagerly ate a fresh House-Sparrow's egg, which I removed before he had finished it; smelt and refused a piece of duck meat and the above eggs again, also a Spotted Flycatcher's, but readily went on with the Sparrow's egg and licked it out well; again refused duck meat, but returned to his licking of the Sparrow's egg; yet again refused all and the meat, but again returned to the crunching and licking of the Sparrow's egg.

In the evening he showed a marked preference for beef (for which he was, and always is, most eager, though it is not his natural prey) as against duck meat.

Probable order: (1) Egg of House-Sparrow; beef. (2) Duck meat; eggs of Domestic Duck, Eider, Wren, Pied and Grey Wagtails, Willow-Warbler, Great Tit, Spotted Flycatcher.

Expt. 21. July 1, late forenoon. *Does the unpleasant Quality reside in the Yolk or the White?*—Ate a little fresh duck's egg, then smelt and refused both fowl's egg and the duck's; though he certainly, I thought, appeared a little more attracted by the latter. Smelt and refused Great Tit's egg and both fowl's and duck's eggs, but readily ate a Spotted Flycatcher's. Smelt and refused eggs of Great Tit, Wren, fowl, duck, and Pied Wagtail (freshly opened), but ate a Grey Wagtail's (long-opened); smelt and refused again the five species just enumerated, but ate a *freshly*-opened Grey Wagtail's; smelt and refused the duck's egg and some of the white poured out into a spoon, but readily ate its *yolk* from a spoon, licking it out very assiduously; smelt and refused (licked up a *very* little before rejecting)

the white of a fowl's egg, but readily ate its yolk, licking it clean; licked once or twice into the white of a Wren's egg offered similarly in a spoon, but quickly desisted and withdrew, and, sometimes smelling it (when I pressed it on him), refused it as persistently as he had already done the whites of the fowl's and duck's. I then offered the broken shell of the Wren's egg, containing now only the yolk, and he merely licked it once and withdrew. I then turned the yolk out into a spoon and it was smelt and eaten, though just possibly, I thought, with not quite the appreciation shown for the other two.

Order of preference: (1) Spotted Flycatcher, Grey Wagtail, and yolks of Fowl's, Duck's, and Wren's eggs. (2) Great Tit, Pied Wagtail, and whites of Fowl's, Duck's, and Wren's eggs.

Expt. 22. July 21, early afternoon.—Smelt and refused Pied Wagtail, Great Tit, and Wren, but readily ate a duck's egg with the yolk mixed up with the white, also a fowl's egg similarly prepared. I did not let him eat a great deal, but he seemed quite prepared to. He then smelt and refused a fowl's egg in which the relative positions of white and yolk were normal, but again readily ate the other, in which they were mixed, also the duck's; smelt and refused the Wren's, Pied Wagtail's, and Great Tit's, also, persistently, a fresh Hedge-Sparrow's, but ate a Spotted Flycatcher's; again smelt and persistently refused the Hedge-Sparrow's and the others already refused, but smelt and ate with real eagerness a House-Sparrow's egg, repeated his refusals, licked a Grey Wagtail's egg from a crack in which the white was flowing, but desisted almost at once and refused it, but ate with as much eagerness as the Sparrow's a not quite fresh Bullfinch's egg.

Order of preference: House-Sparrow and Bullfinch (latter not quite fresh) much more eagerly than (2) Duck and Fowl, with yolk exposed, and Spotted Flycatcher. (3) Fowl's egg with yolk protected by the albumen, Grey and Pied Wagtails, Great Tit, Hedge-Sparrow, Wren. Of these

the Grey Wagtail's was apparently found a little more tempting than the others.

Expt. 23. July.—The first part of the experiment was again a test of addled eggs and eggs with mixed and exposed yolks. Results as before. An interesting point was his refusal of fowls' eggs (several offered), though he had eaten badly in the night (fowl's intestines, which he never cares for, had been given instead of his usual meat and left untouched) and was now hungry enough to attack even Pied Wagtails', Wrens' and Great Tits' eggs, also ducks'. He attacked a fowl's egg, in which yolk and white were mixed. He also attacked a Turtle-Dove's egg (*Turtur auritus*).

He now smelt and refused the duck's egg, licked and refused the Dove's, smelt and refused the same Pied Wagtail's egg as before; but, after smelling it, attacked a Meadow-Pipit's egg; smelt and refused the Pied Wagtail's, but, on my continuing to press it on him finally licked into it and, breaking the yolk, went on with it; smelt and refused a second freshly opened Pied Wagtail's from the same clutch, its yolk well protected by the white, but readily ate a Meadow-Pipit's; smelt and refused the Pied Wagtail's, and this time a Meadow-Pipit's too, also a Garden-Warbler's and the Wagtail's and Pipit's re-offered; but, on smelling it, readily attacked a Greenfinch's. I withdrew it before he had finished it and re-offered the Wagtail's and Pipit's. He smelt and refused each, but accepted readily and finished the Greenfinch's.

He smelt and refused a fowl's egg, then came forward and smelt over the Duck's, a second Fowl's, the Dove's and the addled Moorhen's (all of which had been lying just before him all this time), and licked a little into the last, but desisted; smelt and refused the Pied Wagtail's, licked and refused a Meadow-Pipit's, smelt and refused the Garden-Warbler's, a Grey Wagtail's, and a Wren's; licked and refused one of the Meadow-Pipit's (of which the sides were now broken away, showing the yolk right on the surface, but still unbroken); and smelt and refused a cracked

Yellow-Hammer's egg, the white of which was oozing out most temptingly as I held it to him. This egg fell accidentally at his fore feet where he was lying, and he stooped, tasted, and refused it, began to lick up the contents of a Dove's egg in which the yolk had become mixed with the white, refused (first smelling it) the other Dove's egg in which these were separate, and returned to his eating of the first. He then repeated all his previous refusals, but readily attacked a Greenfinch's egg and, on my withdrawing it, followed it out of his sleeping-box—a thing he had done to no other egg in this experiment; again repeated his refusals, including fowl, but was rather inclined to eat the fowl's egg in which yolk and white were mixed.

That he was still not replete was shown by his eating half a not irreproachable Guillemot's egg. The few offerings that closed the experiment once more included eggs that were not fresh, so that they are again hardly worth detailing. A Greenfinch's egg was attacked when the Guillemot's, mixed Dove's and other eggs were being refused. A fowl's head was also refused, but beef would certainly have been eaten.

Order of preference: (1) Greenfinch. (2) Fowl and Dove, in which yolk was mixed with white. (3) Meadow-Pipit. (4) Duck, Turtle-Dove, Grey Wagtail, Pied Wagtail, Wren. Yellow-Hammer comes in (3), (4), or (5). (5) Fowl, unmixed. (6) Fowl's intestines, placed below Fowl's egg on previous night and other occasions.

Apart from the preferences, three points were interesting. These were (1) the mongoose's greater dislike for the white, seeming to show that the albumen is rather specially the carrier of the egg's defence; (2) his readiness to eat stale eggs—he even showed preferences as between species that were apparently equally stale; and, (3), a possible special repugnance to fowls' eggs as a result of having had to feed on them alone on the previous night. I have seen a similar repugnance in insectivorous birds towards an insect of which they had just been given too exclusive a supply.

All the eggs used were non-incubated.

Expt. 24. July 17.—Offered the mongoose a duck's egg. He began to lick at its contents. I withdrew it and offered a fowl's egg. He smelt and refused it. I put it down in front of him, and he gave one or two licks at it and desisted. I put a duck's egg beside it. He came forward again, smelt it, was somewhat more inclined for it, and licked into it a little; then desisted, drew back and lay down again. After this he refused to be tempted by either egg. I left each in front of him—just outside his sleeping-box door, he lying just inside—and offered (in my fingers as usual) a Guinea-fowl egg (*Numida meleuigris*). He smelt it well, licked it, became intensely interested, and began to follow it out on my withdrawing it. I re-offered, in my fingers, the fowl's and duck's, and he would touch neither, but at once commenced to lick at the Guinea-fowl's. I withdrew it again, and again left the fowl and duck egg before him. He smelt each and withdrew. I then put down the Guinea-fowl egg a little distance on *my* side of the other two. These were side by side, and, with some straw he had thrown out of his box, formed a barrier between the mongoose and the Guinea-fowl egg. He at once rose and came forward, smelling the fowl and duck eggs as he did so, then leaned right over them in a very strained position, and began eagerly to lick up the Guinea-fowl's. He soon drew back, and, in doing so, actually licked and refused the fowl's egg, shaking his head vigorously, and smelt and refused the duck's; and, making quite a *détour*, came round to my side of the Guinea-fowl egg and began to lick it out in comfort. He had half finished it, or rather more, when he began to find the opening too small and tried to enlarge it. Whether because the shell was excessively hard, or for some other reason, he quitted it after licking very little more and began to lick at the fowl's egg instead, appetized thereto, as I thought, by his previous feed of Guinea-fowl's egg. I now left, leaving the three eggs in with him for the night. Actually two fowls' eggs had been used, but only one was now left in.

Expt. 25. July 18.—The Fowl's egg has been licked clean

out since last night, the Guinea-fowl's egg remains slightly more than half empty, and I cannot at present examine the duck's egg without disturbing the mongoose, as he has carried it into his sleeping-box and is lying on it. It would almost seem that the Guinea-fowl's egg proved less agreeable than its promise. All the eggs were new-laid, and in last night's experiment, as always, I broke a hole in each before offering it. In breaking I always use a separate implement (nail) for each egg to avoid transferring smells.

Expt. 26. July 26.—To-night, for the third time since the experiment of the 17th, I tested fowl's egg against Guinea-fowl's. Each time the result has been a preference for the former—just the reverse of what occurred in the original experiment.

Expt. 27. Aug. 13.—The mongoose refused a fowl's egg, and, on my leaving it in, tried it waveringly and at once withdrew. He tasted a Guinea-fowl's egg and refused it, and ignored both eggs on my putting them in with him. Shortly after he again waveringly smelt and tasted them, probably nearly hungry enough, and carried the Guinea-fowl's egg into his sleeping-place, but there at once abandoned it, and came out and remained outside, taking no notice of either egg. I therefore recovered both eggs and held each to his nose in turn. He gave a lick at each (each was, as usual, holed) and withdrew; but on my holding a fresh Bullfinch's egg to him (laid in captivity) he smelt and at once attacked it with the greatest eagerness.

I withdrew it and re-offered the other two eggs. He persistently refused both; but, on my substituting once more the remains of the Bullfinch's egg, he attacked it with as great eagerness as previously, and, when he was unable to extract anything more from it, eagerly crunched up the shell as well.

Expts. 28 and 29. Aug.—At a later date I carried out two separate experiments with another fresh Bullfinch's egg. Each time the result was: smelt and refused and tasted and refused fowl's egg and Guinea-fowl's egg, but readily ate

Bullfinch's. The eggs were, as usual, broken into by myself before being offered, in order to avoid complications through differing strength of shell.

CONCLUSIONS FROM EXPERIMENTS ON THE MONGOOSE.

No one can read these experiments, I think, without realizing that preferences of the most marked kind were shown. At the same time, the change that occurred in the mongoose's opinion of one or two eggs warns us that his "placings" in these experiments do not necessarily, in every case, represent what his final verdict on the eggs would have been had he been supplied with more abundant material. Also, the mongoose's preferences were not necessarily those that would have been shown by Palearctic eaters of eggs, though the analogy of insect-, meat-, and plant-eating vertebrates suggests that the difference would not have been great.

Still, the preferences shown are, perhaps, worth roughly tabulating. The following may be nearly correct:—

1. House-Martin, House-Sparrow, Bullfinch, Greenfinch. Beef.
2. Quite a gap. Mouse, yolks of certain eggs, incubated Black-bird, Kestrel, and Garden-Warbler. Some of the stale eggs of June 30th (as Sandpiper, Golden Plover, Grouse, Pheasant Oystercatcher) come here or higher*.
- Lesser { 3. Song-Thrush, Spotted Flycatcher, Meadow-Pipit.
- White- { 4. Hedge-Sparrow. } Domestic Duck and Turtle-Dove hereabouts.
- throat, { 5. Grey Wagtail. }
- Yellow- { 6. Pied Wagtail, Domestic Fowl. }
- Hammer. { 7. Wren, Willow-Warbler, Guinea-fowl (at the last). } Great Tit.
8. Fowl, temporarily.
9. Fowl's intestines, Burnet Moth.

All these eggs, with the exceptions stated in Grade 2, were fresh and non-incubated.

The special dislike for the albumen of the low-placed eggs was of interest, as suggesting the part of the egg which

* Red Grouse "with definite eagerness" and "all I would allow" of each of the others here mentioned.

(if these views be correct) is specially entrusted with its defence—at any rate in relation to an Indian Mongoose.

The mongoose's daily food during the two months was mainly meat—raw beef (almost daily), frequent heads of chickens and ducks, young chicks, &c., that had come to an untimely end, sometimes mice and on a few days rabbit. He also received occasional insects (chiefly Noctuid moths); scraps; and an egg every night—not entirely fowls', for I had some other eggs, of doubtful freshness, that I did not use in experiment (except where specially mentioned) but utilized for food.

EXPLANATION OF PLATE XIX.

The figures of South-African eggs are intended to illustrate:—

- a. Polymorphism in Weavers' eggs and their tendency to fall into local colour-groups with unrelated eggs (i. e., *Hyphantornis jamesoni*, figs. 3, 5, 7, 9, 12, 15).
- b. The considerable pigmentation of some eggs laid in holes (i. e., *Spreo bicolor*, fig. 18).
- c. The extraordinarily close resemblances that purely coincidental variation can bring about.

Fig. 1. *Tympanistria bicolor*.

2. *Colius striatus minor*.

3. *Hyphantornis jamesoni*.

4. *Crateropus kirki*.

5. *Hyphantornis jamesoni*.

6. *Dryoscopus guttatus*.

7. *Hyphantornis jamesoni*.

8. *Laniarius quadricolor*.

9. *Hyphantornis jamesoni*.

10. *Pycnonotus layardi*.

11. " "

12. *Hyphantornis jamesoni*.

13. *Pycnonotus layardi*.

Fig. 14. *Pycnonotus layardi*.

15. *Hyphantornis jamesoni*.

16. *Pycnonotus layardi*.

17. *Anthus lineiventris*.

18. *Spreo bicolor*.

19. *Erithacus swynnertoni*.

20. *Cossypha natalensis*.

21. *Sitagra velatus*.

22. " "

23. " "

24. " *xanthoptera*.

25. " "



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SOUTH AFRICAN BIRDS' EGGS.